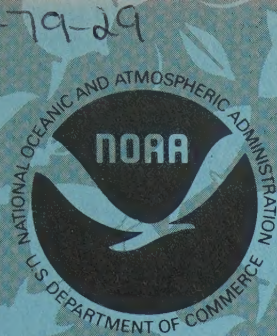


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GROWTH & REPRODUCTIVE RATES IN
TWO POPULATIONS OF SPINNER
DOLPHINS, *Stenella longirostris*, WITH
DIFFERENT HISTORIES OF EXPLOITATION

BY
WILLIAM F. PERRIN & JOHN R. HENDERSON

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Growth and reproductive rates in
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ABSTRACT

A model of density-dependent change in net reproductive rate has been used in assessing status of dolphin stocks in the eastern tropical Pacific. The eastern spinner population has been estimated to be at a lower fraction of original size (38-83%) than is the population of whitebelly spinners (71-94%). Higher reproductive rates would be expected in the former than in the latter on the basis of the density-dependent model. Based on analyses of over 4,000 specimens collected through 1978: (1) there is a relative paucity of fully adult males in the eastern population (possibly indicating lower average fertility), (2) the eastern spinner female attains sexual maturity about one tooth-layer unit (GLG, probably one year) earlier than does the whitebelly spinner, (3) ovulation rate and pregnancy rate in young females are lower in the eastern population (possibly because of the low number of fully-adult males) and (4) the proportion of all females which are sexually mature is lower in the eastern population (possibly indicating a shift in age structure toward younger animals). Gross annual reproductive rates (proportion female x proportion of females mature x pregnancy rate) are not different in the two populations (about 8-10% in both cases). The results of the comparison do not confirm the assumption of density-dependent increase in gross reproduction.

INTRODUCTION

Tuna seiners operating in the eastern tropical Pacific (ETP) kill dolphins incidentally during fishing operations (Perrin, 1969; Fox, 1978). The incidental kill has reduced the abundance of some geographical forms, by as much as nearly one half (Southwest Fisheries Center, 1976; revised and updated estimates in NOAA 1977). The basic model used in assessing the status of stocks and estimating net production has been based on density-dependent change in production, i.e., that reproductive rates go up as density goes down (loc. cit.). Such change has not been observed in a dolphin population; its use in dolphin assessment and management has been based on observations of populations of terrestrial mammals, pinnipeds and two baleen whales (Fowler, 1979). This paper presents the results of a comparative study of two populations estimated to be at different proportions of their initial sizes, in an attempt to validate the assumption of density-dependent change.

At least four morphologically differentiated stocks of spinner dolphins, *Stenella longirostris* (Gray, 1828), exist in the eastern tropical Pacific (Perrin, 1975a & b; Perrin, Sloan & Henderson, 1979; and Au, Perryman & Perrin, 1979). The two forms treated in this paper are the "eastern spinner dolphin", which occurs from close to the coast of Mexico and Central America to several hundred kilometers offshore, and the "northern whitebelly spinner dolphin", which is a more high-seas form, found north of the equator ranging west to about 150° W. long. At the end of 1977, the population of eastern spinners was estimated to be 38 to 83% (central estimate 55%) of its initial size, whereas the population of whitebelly spinners (including both of the since-recognized "northern" and "southern" stocks -- Perrin et al. 1979) was estimated to be 71 to 94% (central estimate 80%) of initial size (NOAA, 1977). In assessment and management of the ETP dolphin stocks, maximum net productivity (in numbers of individuals) has been assumed to occur at population size somewhere between 50 and 60% of initial size. If the central estimates are accurate and the assumption is valid, and if it be assumed that the two populations had similar initial reproductive rates and that density-dependent changes would occur in reproductive rates, then reproductive rates should be higher in the eastern population than in the northern whitebelly population.

MATERIALS AND METHODS

The Field Program

Most of the data and specimens were collected by NMFS scientific technicians aboard commercial tuna seiners. The collection procedures were the same as previously described for the spotted dolphin (Perrin, Coe & Zweifel, 1976). Data were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, 30 in 1975, 48 in 1976, 72 in 1977, and 74 in 1978. Some specimens were also collected by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

The Sample

In 1971 and early 1972, when the field program was very limited, adult female specimens were preferentially selected for dissection when available, and the samples for those periods are therefore biased with respect to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was practiced in determining which animals were to be examined, and those samples are assumed to be cross-sectional with respect to the kill (and with respect to the the population). Fetuses were not collected in 1968.

The sample of animals for which life history data including, but not limited to, sex and body length were collected includes over 4,000 specimens. Length-frequency data by month and sex were presented for eastern spinner specimens collected before 1976 in Perrin et al. (1977); length-frequency data for the balance of the eastern spinner material (1976-78) and the whitebelly spinner specimens are presented in Figures 1 and 2. Charts showing collection localities are presented in Henderson, Perrin & Miller (1979). Identification of specimens to race. The morphological differences between the two races of spinner dolphins are modal, and their geographical ranges overlap, so schools and single-school groups of specimens are identified at

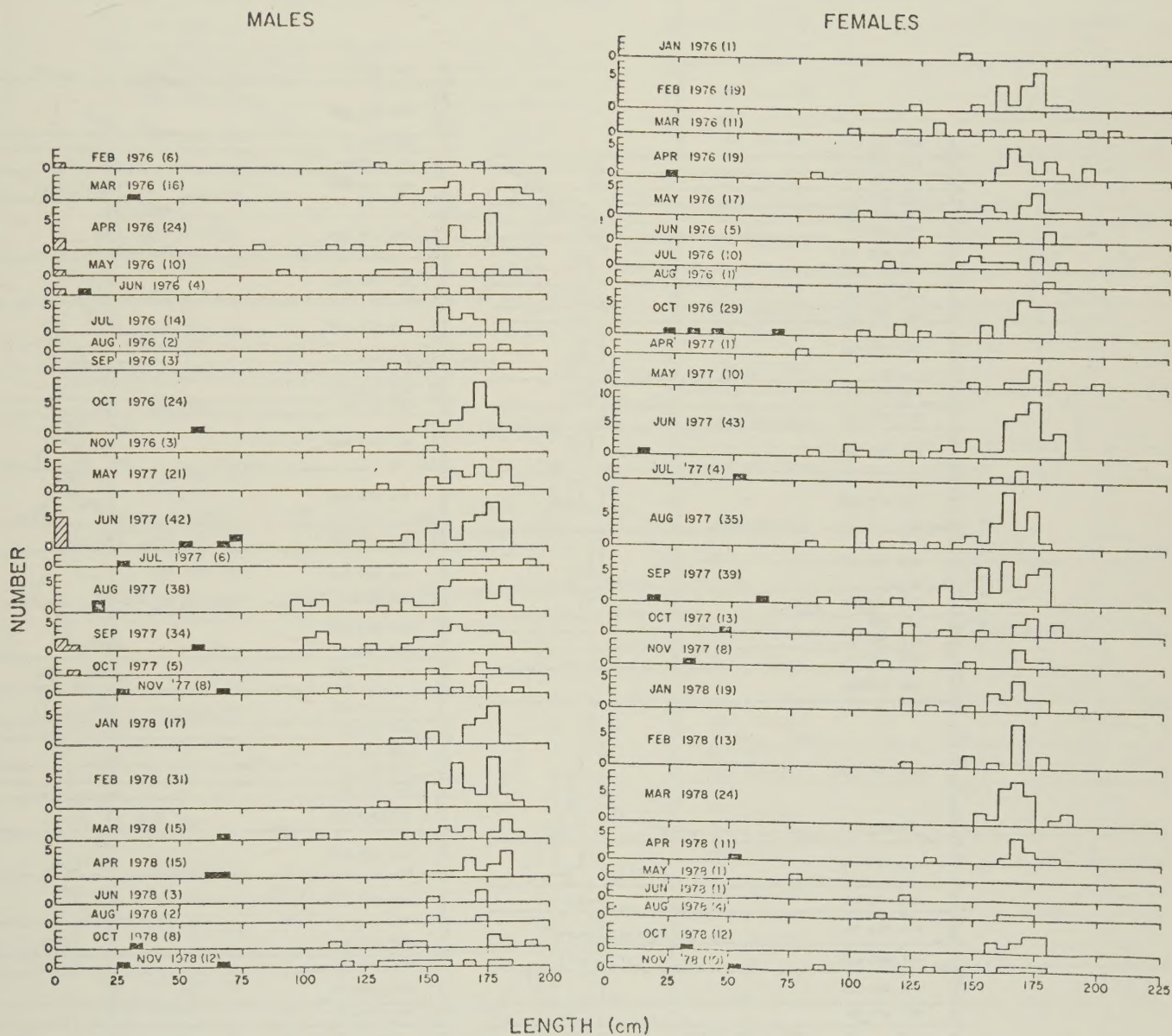


Figure 1. Length frequency distributions by month and year eastern spinner dolphins collected 1976-78 and included in the present study. (Size samples in parentheses) Solid squares represent fetuses; hatched squares represent fetuses of undetermined sex (plotted with males)

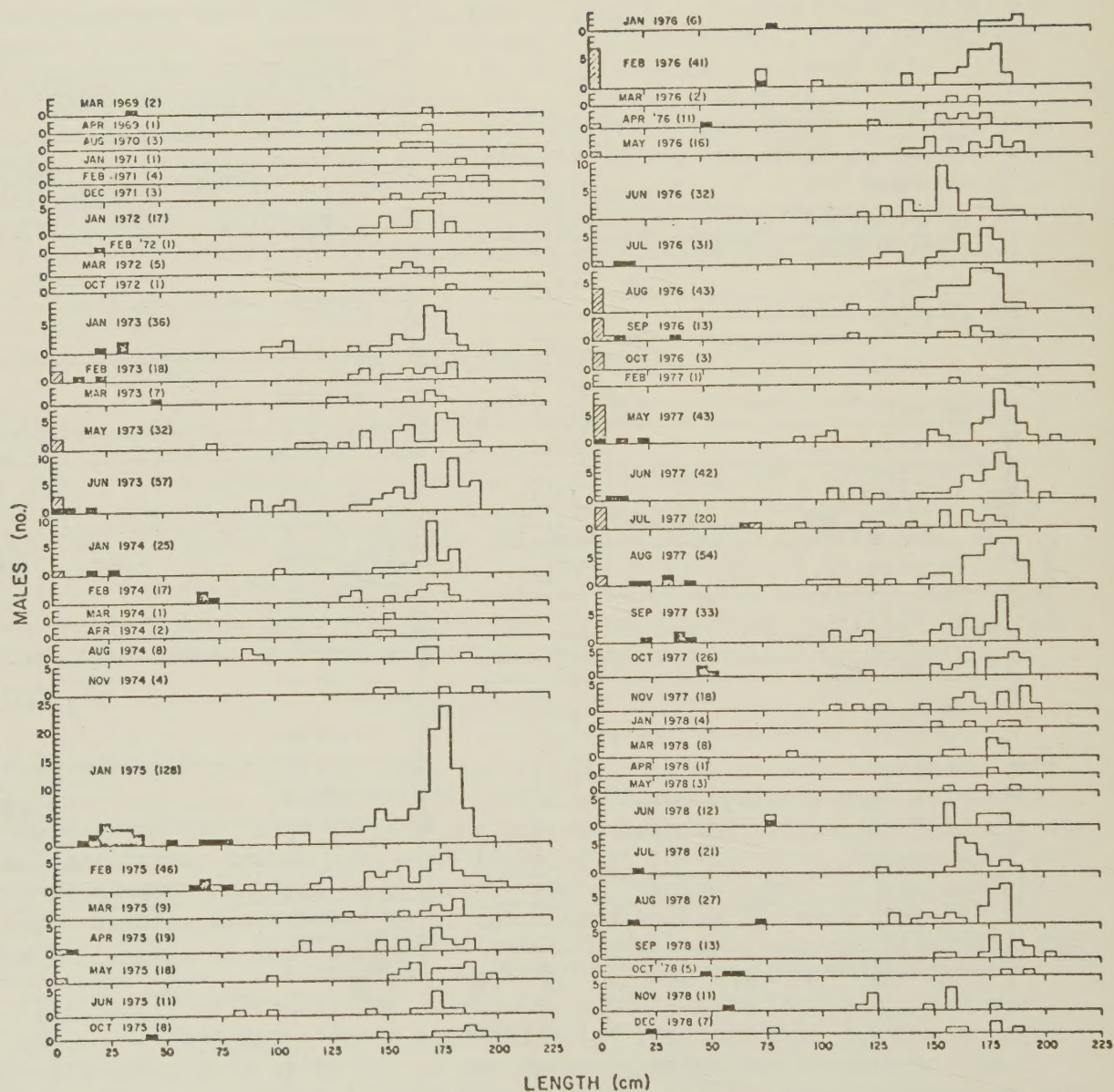
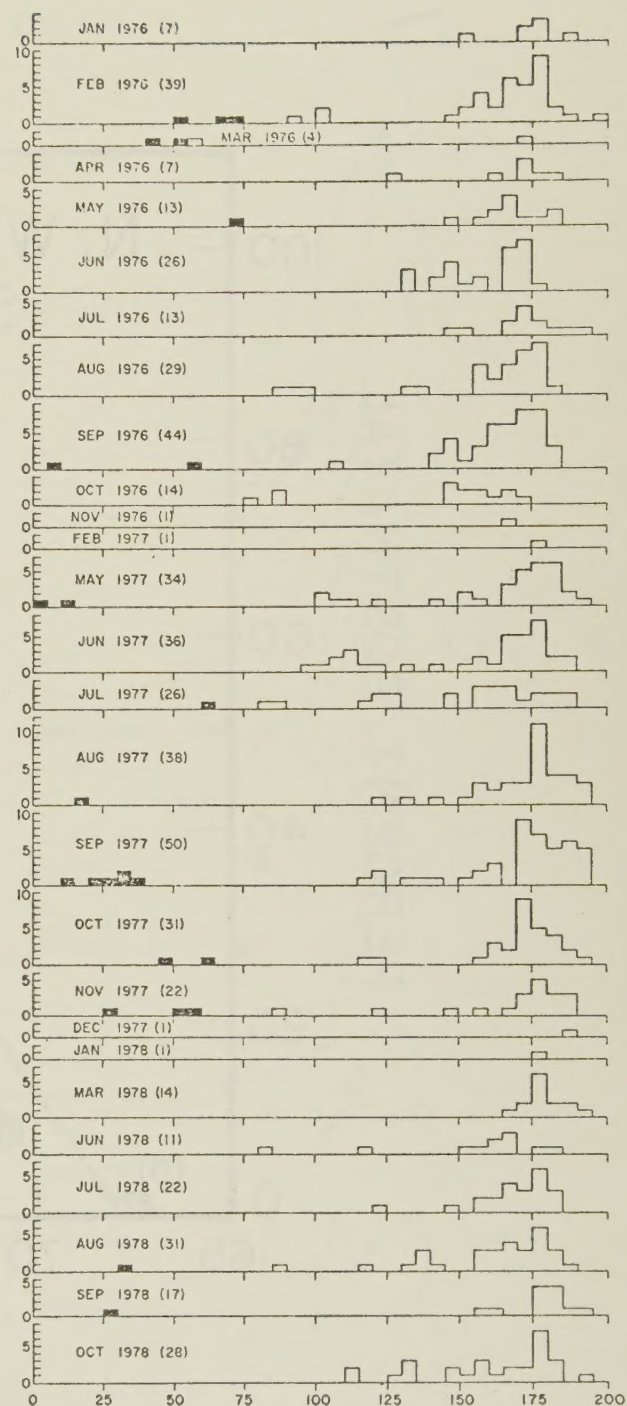
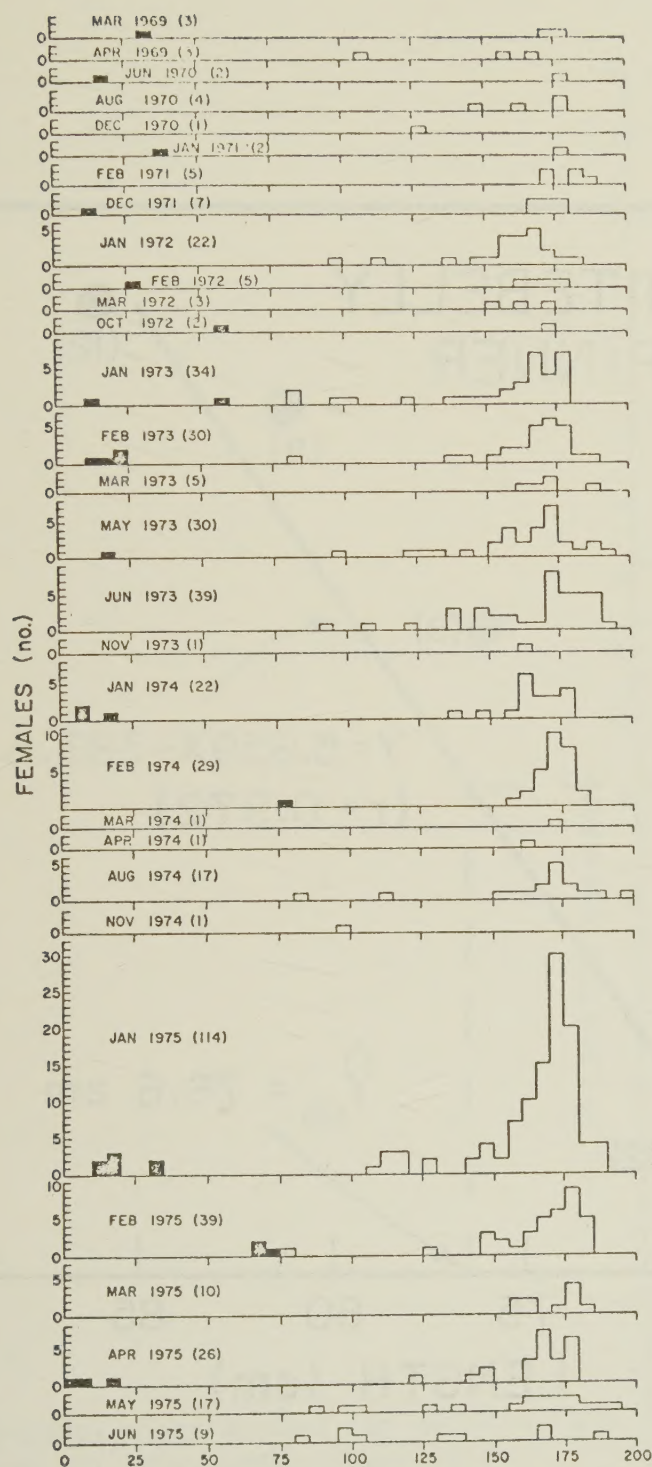


Figure 2. Length-frequency distributions by month and year of northern whitebelly spinner dolphins collected 1969-78 and included in the present study. (Sample sizes in parentheses)
A. Males



LENGTH (cm)

B. Females

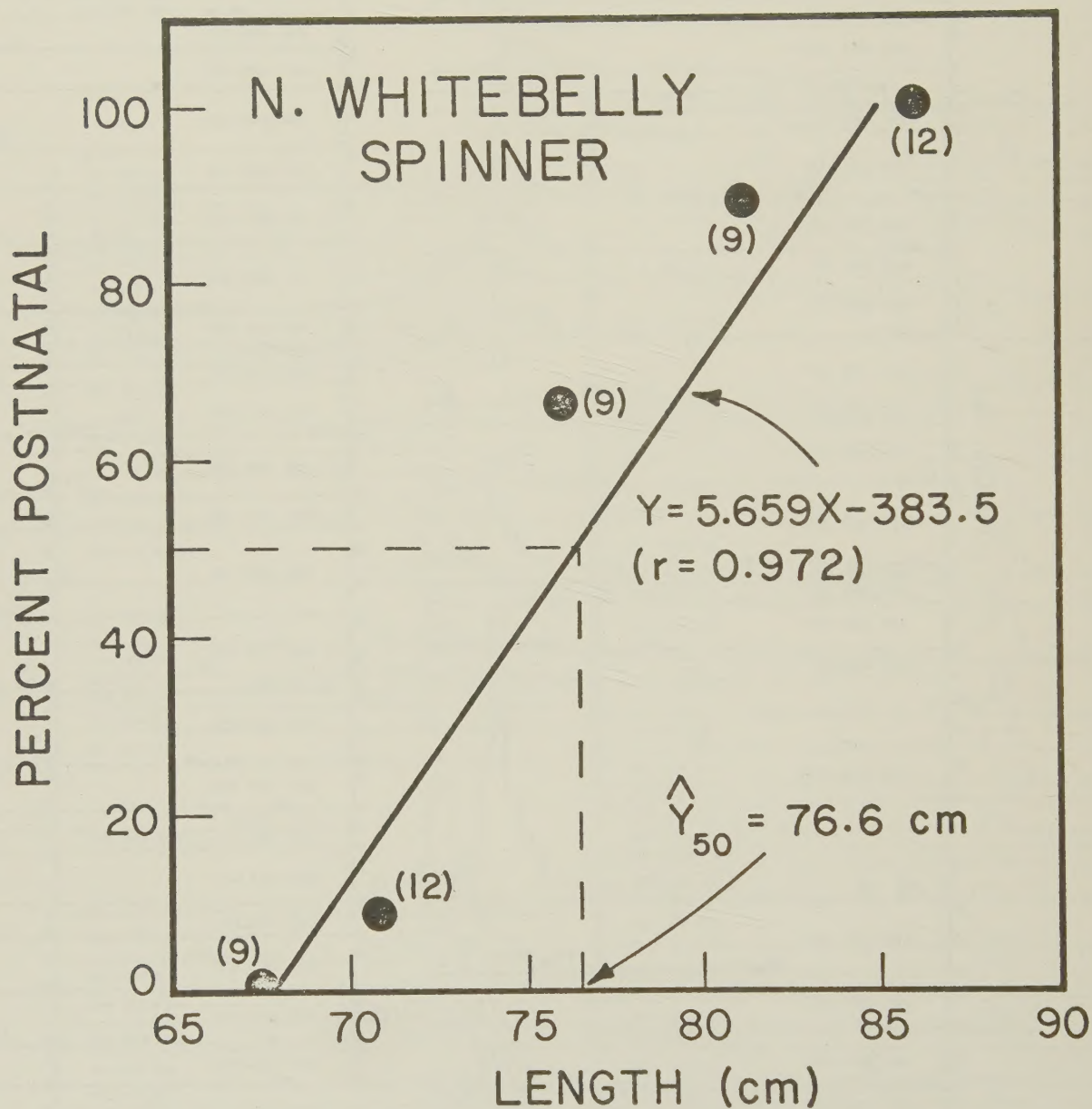


Figure 3. Estimation of average length at birth, based on unweighted linear regression of percent postnatal on body length, in 5-cm increments, for 51 specimens of the northern whitebelly spinner dolphin (24 fetuses & 27 calves) between 65 and 89 cm long.

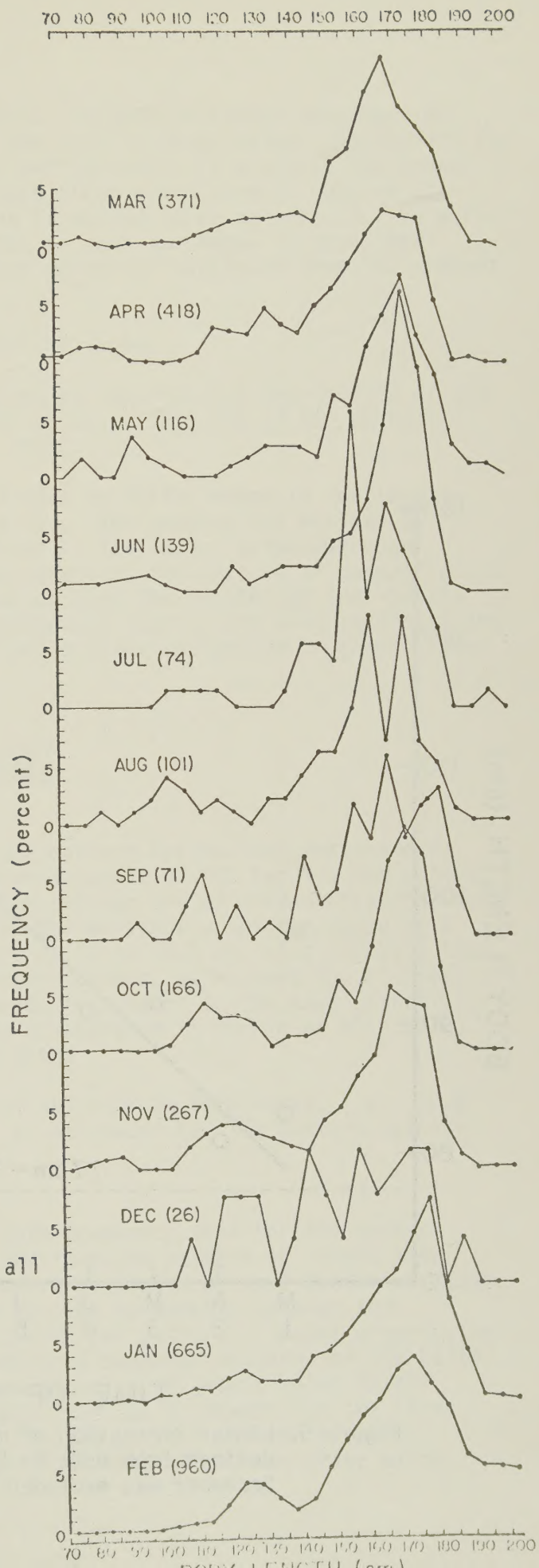


Figure 4.

Length-frequency distributions. by month for all years pooled, of body length in postnatal eastern spinner dolphins. (Sample sizes in parentheses)

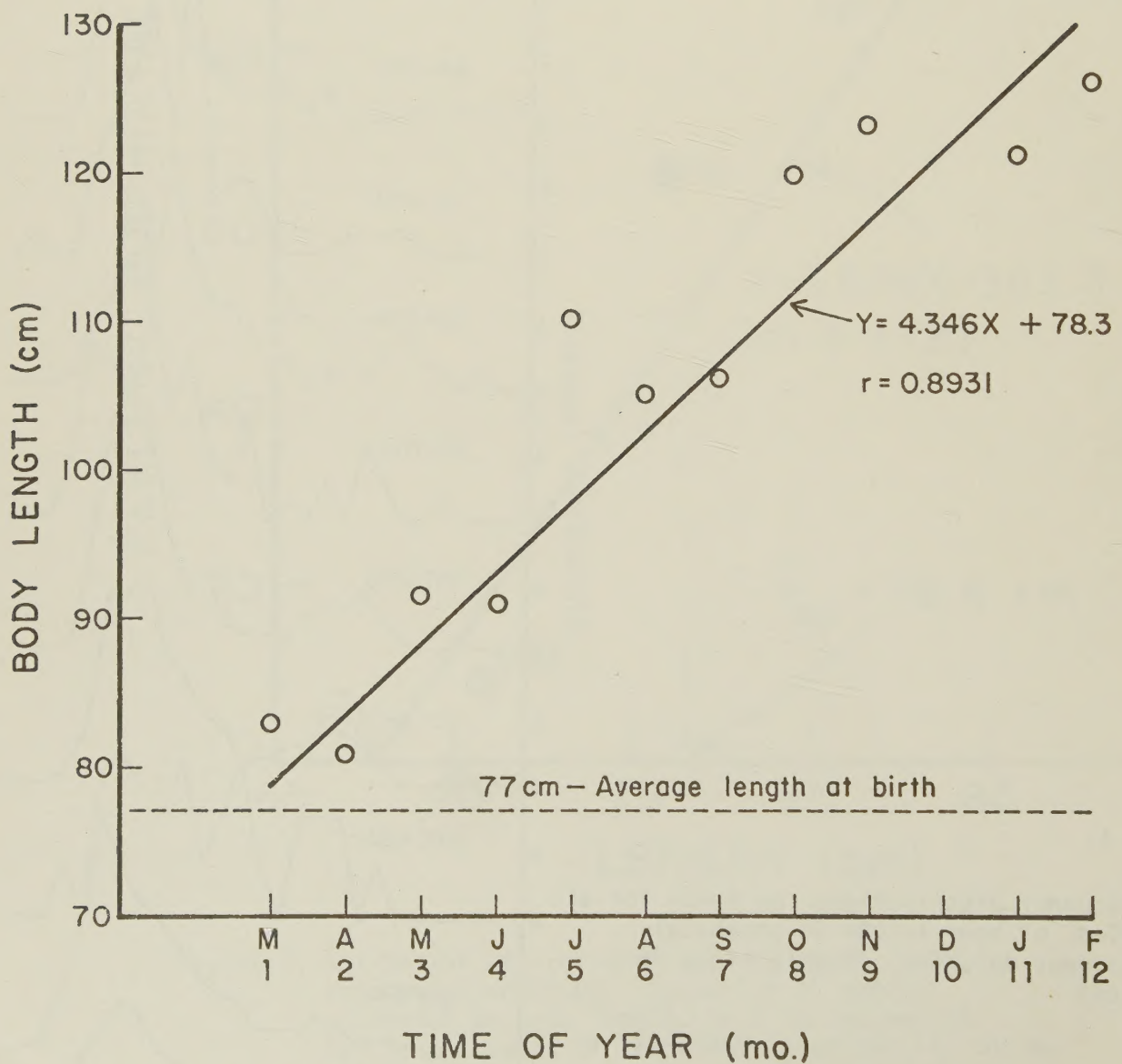


Figure 5. Linear regression of mean of body-length modes (NORMSEP-defined from data in Figure 4) on month of year. December was excluded because of small sample size.

sea based on their modal characteristics. In case of single specimens or small series of specimens coming from the area of geographical overlap and for which information on the nature of the entire school is minimal, the danger exists of erroneous identification. Such error would tend to obscure any differences between the two populations in reproductive parameters. We were conservative in reviewing identification of such specimens to race, and designated many as "unidentified spinner dolphins" (excluded from the present study).

Laboratory Procedures

Laboratory procedures were the same as reported for the studies of the eastern form of *S. longirostris* (Perrin et al., 1977) and of the spotted dolphin, *S. attenuata* (Perrin et al., 1976).

The NORMSEP computer program was used to define modes in the length-frequency distributions for eastern calves. The program was written by Hasselblad (1966) and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates the mixture of normal length distribution into its components, assuming that the lengths of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained that would allow estimation of growth rates in juveniles.

RESULTS

Growth

Length at Birth

The average length at birth in the eastern spinner was estimated by Perrin et al. (1977) at 76.9 cm based on a sample of 101 fetuses and calves, including 23 specimens of the whitebelly spinner and 23 unidentified to race. We estimated average length at birth in the whitebelly spinner based on a sample of 51 fetuses and calves (Figure 3) to be 76.6 cm, statistically the same result. As was done for the eastern spinner, we rounded the estimate off to 77 cm in analyses below. The estimate is subject to the same potential biases as that for the eastern spinner (elaborated in Perrin et al., 1977).

Length of Gestation and Fetal Growth Rates

We assumed these parameters to be the same in both forms, i.e., 10.6 months and 8.37 cm/mo (linear phase), as estimated for the eastern spinner.

Postnatal Growth

Perrin et al (1977) examined length frequency data for the eastern spinner (data from 1975 and earlier) and found no pattern of length mode progression. Growth rates were therefore estimated by more deductive means. We examined the length frequency data for the whitebelly spinner and encountered a similar situation, i.e., no clear pattern of modal progression with season, this in spite of the finding of seasonal patterns in the birth dates by Barlow (1979). However, re-examination of growth rates in the eastern spinner based on a larger sample than was available for the first study (including data from 1976, 77 & 78) did yield a pattern of modal progression (Figure 4) covering a span of at least 12 months after birth.

A linear regression of the NORMSEP-defined (see Materials and Methods) means by month of the progressing mode of calves (Figure 5) on month of year yields an estimated average growth rate for the first year of 4.35 cm/mo and an average length at one year of 129.2 cm.

Length Relative to Tooth Layering

Perrin et al. (1977) presented growth curves and equations for the eastern spinner in terms of length relative to number of postnatal dentinal growth layer groups (GLGs, terminology of Perrin & Myrick, 1980, = dentinal layers in terminology of Perrin et al. 1977). We examined relationships between GLGs and length for 170 male and 232 female northern whitebelly spinners (Figure 6). The sub-samples for age determination were selected as for the eastern spinner (Perrin et al., 1977).

We fit curves to the single-GLG means using a two-cycle model as was done for the eastern spinner (loc cit; see Zweifel & Perrin 1980 for rationale & details of method), with some differences: (1) The upper end of the second-phase curve (asymptotic length) was estimated in the iterative fitting procedure because asymptotic length estimated as it was for the eastern spinner, as the average length of the few very old (13 GLGs) specimens in the samples for both sexes, was lower (by 16 mm in females) than the average length of adult animals, probably a statistical artifact. The procedure resulted in estimates of asymptotic length close to the average sizes of adults (for example, 174.9 cm vs. 175.2 cm in the females). (2) In the eastern-spinner analysis, animals with ≥ 13 GLG's were pooled into a single stratum. In the present analysis of growth of the whitebelly spinner, because of a relatively larger number of older specimens -- particularly in the male sample, animals with ≥ 15 GLGs were pooled in the final stratum. (3) For the eastern spinner, male and female juveniles were considered jointly; the respective length/age means coincided almost exactly. For the northern whitebelly spinner, the juvenile means differed between sexes, those for the females being higher than those for the males, and the data for juveniles of the two sexes were therefore fitted separately. Age at shift from the juvenile to "adult" portions of the overall curve (age at onset of the adolescent growth spurt) differed between the sexes. It was 4.34 GLGs in males (rounded off to 4.3 below) and 5.15 GLGs (rounded off to 5.2 below) in females. Estimated lengths at these ages are 157.8 cm (rounded off to 158 cm) and 160.9 (rounded to 161), respectively. The shift for the eastern spinner came at 4.11 GLG's (rounded off to 4 GLGs).

The fitted growth equations for males are,

for juveniles < 4.5 GLG's old,

$$L = 77 \exp \left\{ \frac{0.6897}{0.9455} \left[1 - \exp (-0.9455t) \right] \right\}$$

and, for ≥ 4.5 GLG's,

$$L = 158 \exp \left\{ \frac{0.8262}{1.1173} \left[1 - \exp (-1.1173t) \right] \right\}$$

where L = length in cm

and t = age in GLGs.

For females the equations are, for juveniles with < 5.2 GLG's,

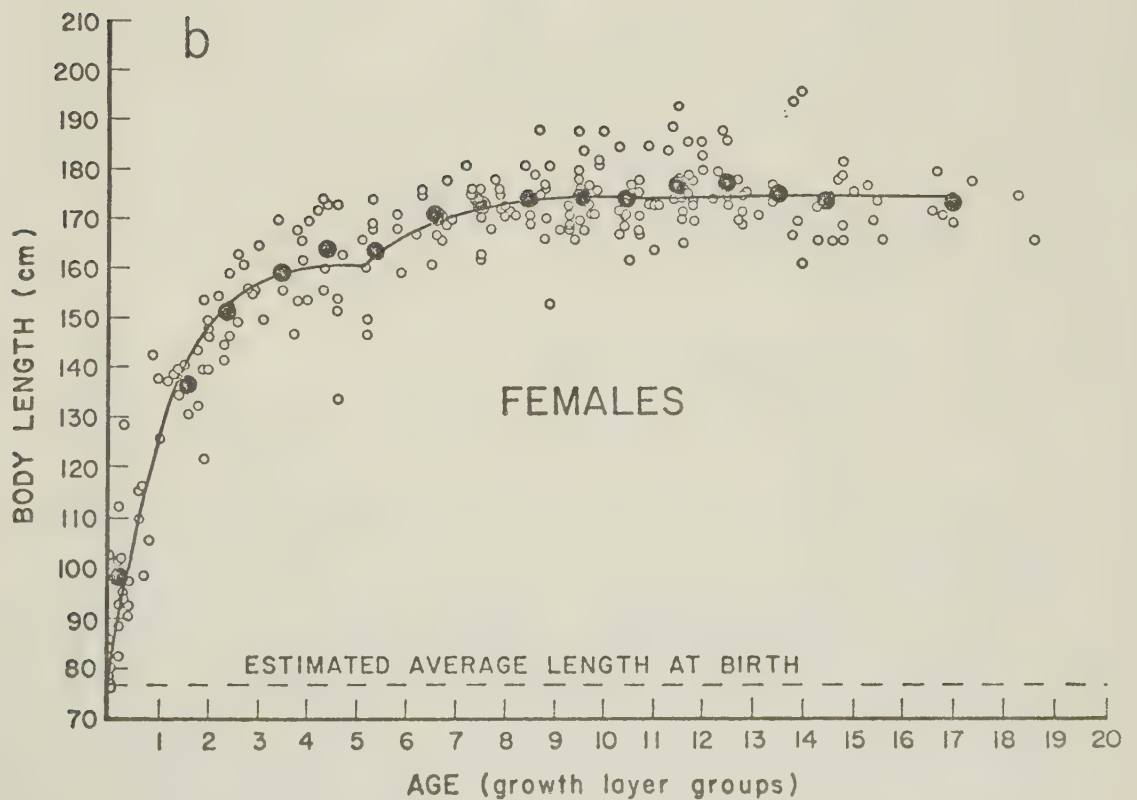
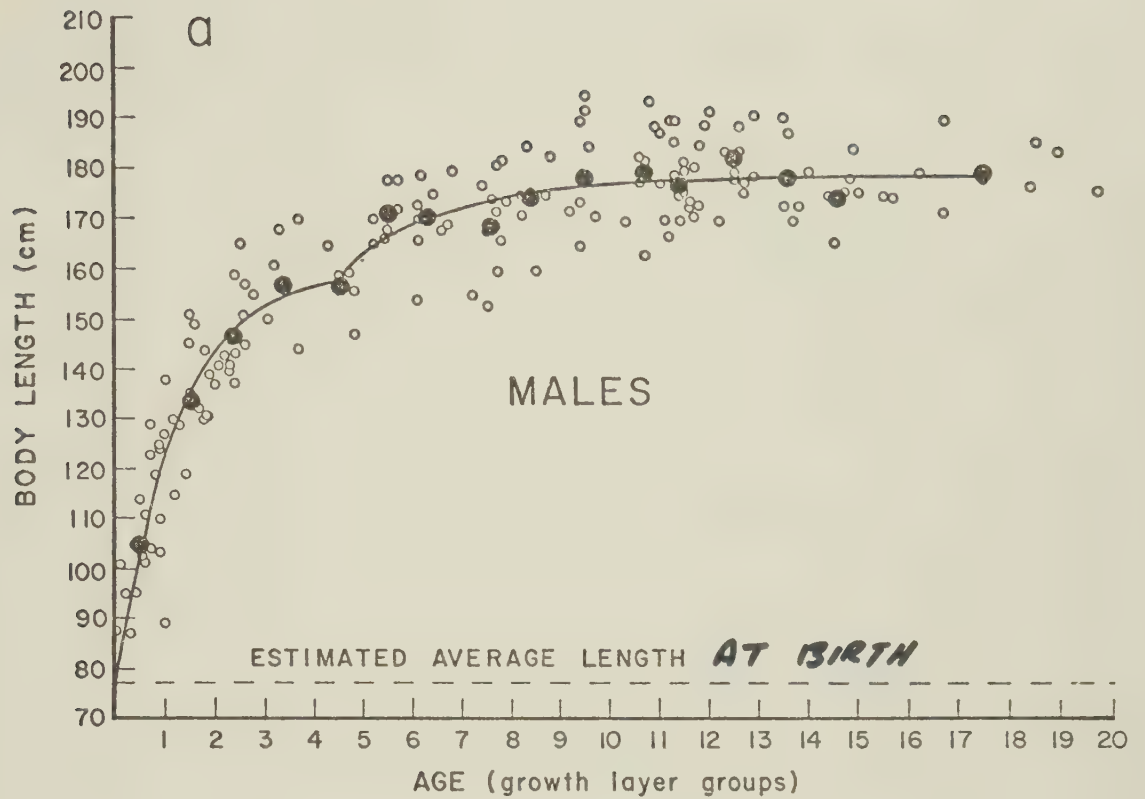


Figure 6. Relationship between body length and age in northern whitebelly spinner dolphins. Lines double Laird-model fits to single-~~contimeter~~
means (see text)

GLG

$$L = 77 \exp \left\{ \frac{0.8262}{1.1173} \left[1 - \exp (-1.1173t) \right] \right\}$$

and, for age ≥ 5.2 GLGs,

$$L = 161 \exp \left\{ \frac{0.0656}{0.7745} \left[1 - \exp (0.7745(t-5.145)) \right] \right\}$$

The equations rearranged and reduced for estimating age from length are:

$$\sigma^{\circ} < 158 \text{ cm}$$

$$t = -1.058 \ln(6.954 - 1.371 \ln L)$$

$$\sigma^{\circ} \geq 158 \text{ cm}$$

$$t = 4.339 - 2.082 \ln(40.542 - 7.813 \ln L)$$

$$\varphi < 161 \text{ cm}$$

$$t = 0.875 \ln(6.874 - 1.352 \ln L)$$

$$\varphi \geq 161 \text{ cm}$$

$$t = 5.145 - 1.291 \ln(60.993 - 11.806 \ln L)$$

Length at one year of age in the eastern spinner was estimated above at 129.2 cm, based on progression of a length mode. That length is achieved at 1.36 GLGs, from the growth equation in Perrin et al. (1977). The previously used estimate of 134 cm (loc. cit.) was deductively derived; corresponding age is 1.57 GLGs, rounded off to the nearest half-GLG to 1.5 GLGs. The new estimate is also close to 1 1/2 GLGs, and that value is used below for both the eastern and the northern whitebelly spinners. Lacking a basis for calibrating the growth curve beyond the first year, we provisionally use below three alternative hypotheses for the rate of GLG deposition:

I. One and one-half GLGs per year,

II. One and one-half GLGs in the first year and one per year thereafter,
or

III. One and one-half GLGs per year until puberty and one per year thereafter.

Adult female northern whitebelly spinners (those of which the ovaries contain at least one corpus of ovulation) average 175.6 cm in length (Figure 7), compared to 171.2 cm for eastern spinners (Perrin et al., 1977), a difference statistically significant at $\alpha < 0.0001$. Length of adult males is more difficult to assess comparatively because of the absence of a clear criterion for attainment of sexual maturity (discussed below in section on male maturation). The difference in length of adult females is reflected in a difference in juvenile growth rates. Size at birth is the same or very nearly the same in the two populations, but juvenile northern whitebelly spinners

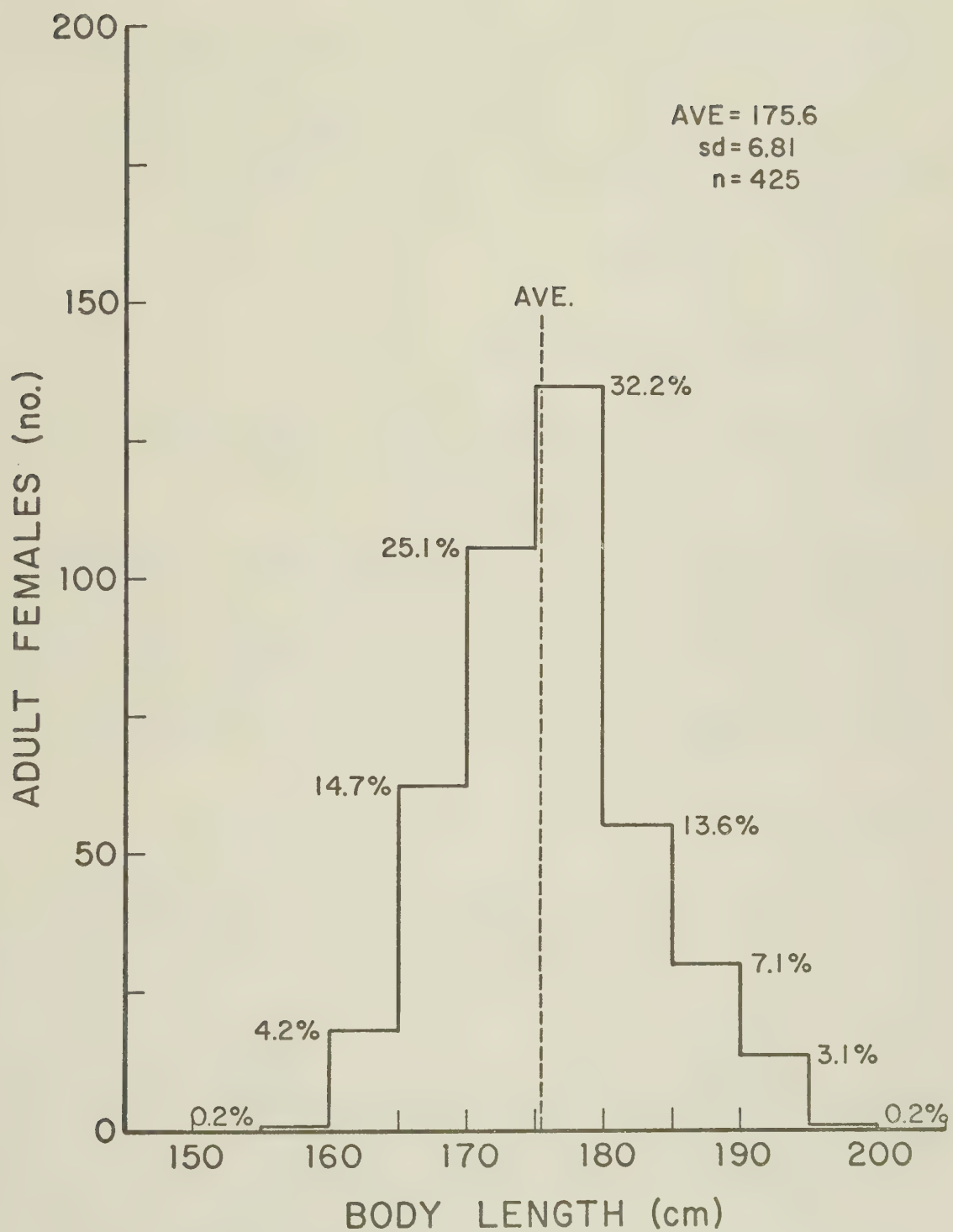


Figure 7. Distribution of length of sexually adult female northern whitebelly spinner dolphins.

grow faster than do juvenile eastern spinners, the difference being most pronounced in females (Table 1).

Table 1. Comparison of juvenile growth rates in female eastern and northern whitebelly spinner dolphins

	Ave.Len.at 4 GLGs	Ave.Len. of Adults
Eastern spinner	156.6 cm ¹	171.2 cm(n=560)
N.whitebelly spinner	159.9 cm	175.7 cm(n=425)
Dif. btwn races	3.9 cm	4.5 c

¹ From new growth equation based on females included in pooled juvenile sample in Perrin et al. 1977: $L = 77 \exp\left\{\frac{0.6521}{0.8984}[-\exp(-0.894t)]\right\}$.

We assessed the statistical significance of the difference between the female juvenile growth trajectories of the two forms with an analysis of covariance, using the linearizing transformation $\ln[-\ln(L/L_{\infty})] = \ln k - \alpha t$, where L was taken to be the average value (161.48 cm + 159.12 cm)/2. The analysis (Table 2) shows the slopes to be significantly different at $0.05 < P < 0.10$ ($F_{1,4}=6.47$). If it is assumed that the slopes are not different, the difference in intercepts ($F_{1,5}=4.3136$) is significant at the same level, $0.05 < P < 0.10$. We thus concluded that the growth curves are different.

Reproduction

The Male

There are marked differences between the two populations in morphological indices of reproductive maturity and function. Average weight of testis (with epididymis) at onset of spermatogenesis is the same in the two populations, 95g (Figure 8) vs 94g (Perrin et al. 1977), but the further course of average testicular development as reflected by the structures of the samples differs sharply between them. In the eastern spinner, proportion of animals with "copious" sperm in the epididymis levels out (at about 50%) at testis-epididymis weight of about 400g (loc. cit.), whereas in the northern whitebelly spinner this occurs at about 200g (Figure 9). In the original eastern sample (Figure 18 in loc. cit.), no testis weighed more than 700 g, and only a very few of that size (but weighing less than 900g) have been collected since. However, a good proportion (>20% at the upper end of body-length size range) of northern whitebelly spinner testes weigh over 700g (up to 1354g in the sample) and all of these examined histologically have had at least "some" sperm in the epididymis. Amount of sperm in the epididymis (possibly indicating degree of fertility) would seem to be positively correlated with testis size, and adult eastern spinners have on the average smaller testes than do northern whitebelly spinners of the same length

(compare Figure 10 with Figure 19 in loc. cit.), even with a 5- cm adjustment for the racial difference in average length of adults, or age (compare Figure 11 with Figure 21 in loc. cit.). At any adult body length (above about 170 cm for eastern spinners and 175 cm for whitebelly spinners) a greater proportion of northern whitebelly spinners attain any particular testis-weight criterion, even the criterion of average weight at first spermatogenesis, and very few eastern spinners attain the high testis weights ($>700\text{g}$) associated with 100% presence of sperm in the epididymis (Figure 12). Three alternative explanations suggest themselves: (1) there is seasonal fluctuation in testis size and the differences reflect seasonal biases in sampling, (2) there are inherent differences between the two populations in male reproductive development and morphology, or (3) testis size (and possibly, male fertility) is depressed in the eastern population, possibly due to some aspect of exploitation.

To address the first of the above possibilities, we examined testis-weight distribution by month for the two populations (Figure 13). The sample sizes are relatively small for some months, but a clear picture of pronounced seasonality emerges nonetheless. In the northern whitebelly spinner, a mode of large-testis-weight animals appears in February, centered around 700-800g. The mode persists through May (although possibly retreating slightly), appears in June centered around 400-500g; moves out to 600-700g again in July-August; and all but disappears in September through January. The months of peak testis weight (and, presumably, peak fertility and breeding) are February and July-August. The eastern spinner also exhibits seasonality (Figure 13b), but with important differences. A mode is present in March-June, centered around 400-500g rather than around 700-800g as in the northern whitebelly spinner. Only a very small proportion of the animals in the seasonally-appearing mode in any month extend above the 700g level, above which all individuals can be expected to have sperm in the epididymis. The apparent dearth of large-testis males, therefore, in the eastern samples is not an artifact of seasonally biased sampling.

The second alternative, that of inherent difference in testis weight, is unlikely because of the similar testis weight at first spermatogenesis and similar adult body length in the two populations and because of the differential pattern of state of the epididymis. Of the three alternatives considered here, the most likely is that of depression of testis weight in the eastern spinner population.

The Female

Attainment of sexual maturity. The smallest sexually mature (possessing at least one corpus of ovulation in the ovaries) whitebelly female encountered was 157cm long, and the largest immature female was 188cm long. This compares to 152cm and 182cm in the eastern spinner (loc. cit.). The differences reflect the above-discussed approximately 5-cm difference in average length of adult females. Average length at attainment of sexual maturity differs between the two populations in the same direction (167.2cm in the northern whitebelly spinner (Figure 14) vs. 164.1cm in the eastern spinner (Figure 22 in loc. cit.)), but the difference (3.1cm) is less than would be expected, yielding a younger predicted average maturation age (from the growth equations) in eastern spinners (5.2 GLGs) than in northern whitebelly spinners (5.9 GLGs). The sigmoid curves of the relationships between body length and

Table 2. Analysis of covariance to test difference between growth curves of female eastern and northern whitebelly spinner dolphins

	d.f.	x^2	xy	y^2	b	Deviations from regression d.f.	M.S.
Eastern	3	5.5935	-3.3140	2.0338	-0.5925	2	0.0352
Northern Whitebelly	3	5.2448	-1.9098	0.7124	-0.3641	2	0.0085
Pooled	-	-	-	-	-	4	0.0218
						1	-
Common	6	10.8383	-5.2238	2.7462	-0.4820	5	0.0456
	-	-	-	-	-	1	-
TOTAL	7	10.8564	-5.1729	2.8899	-0.4765	6	

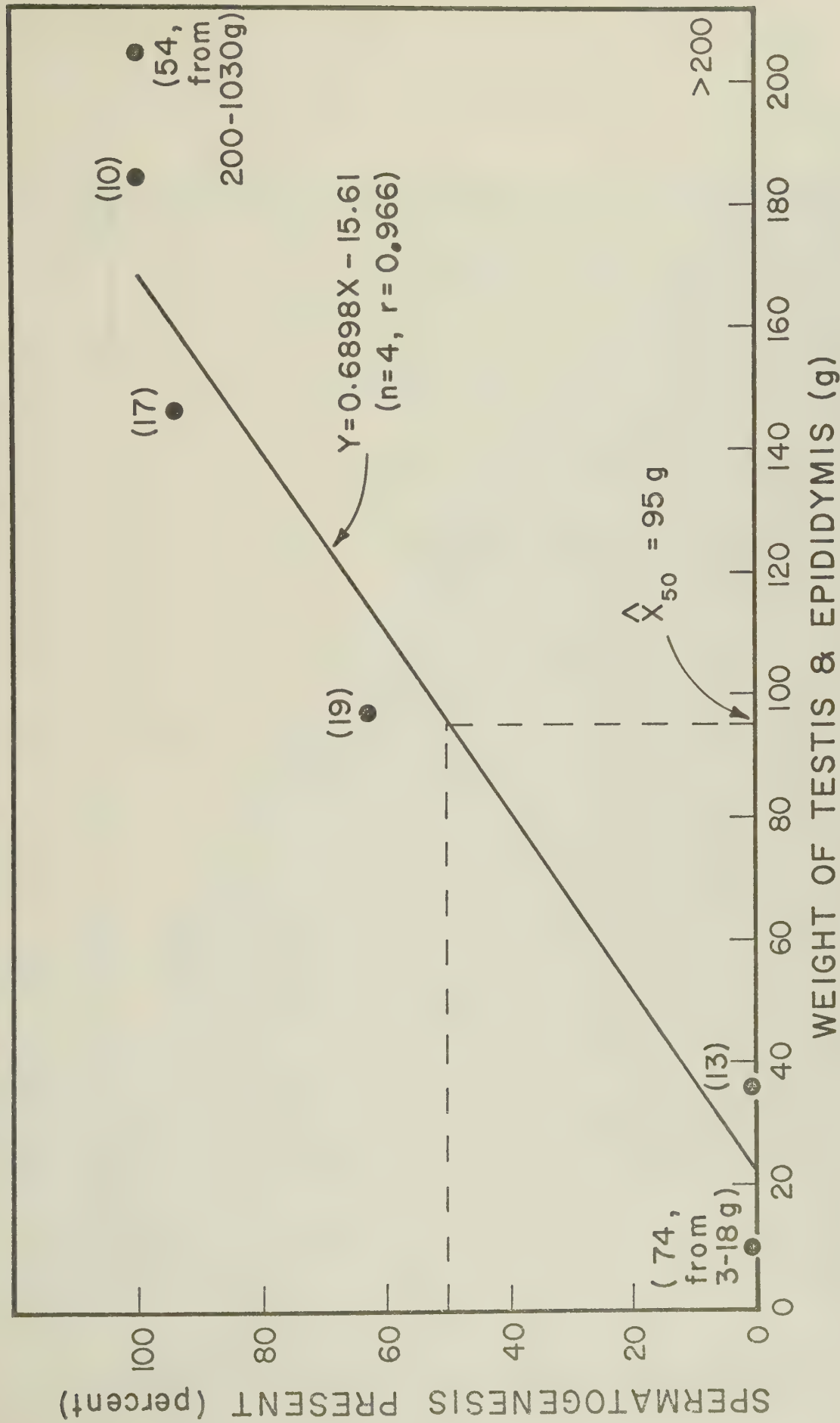
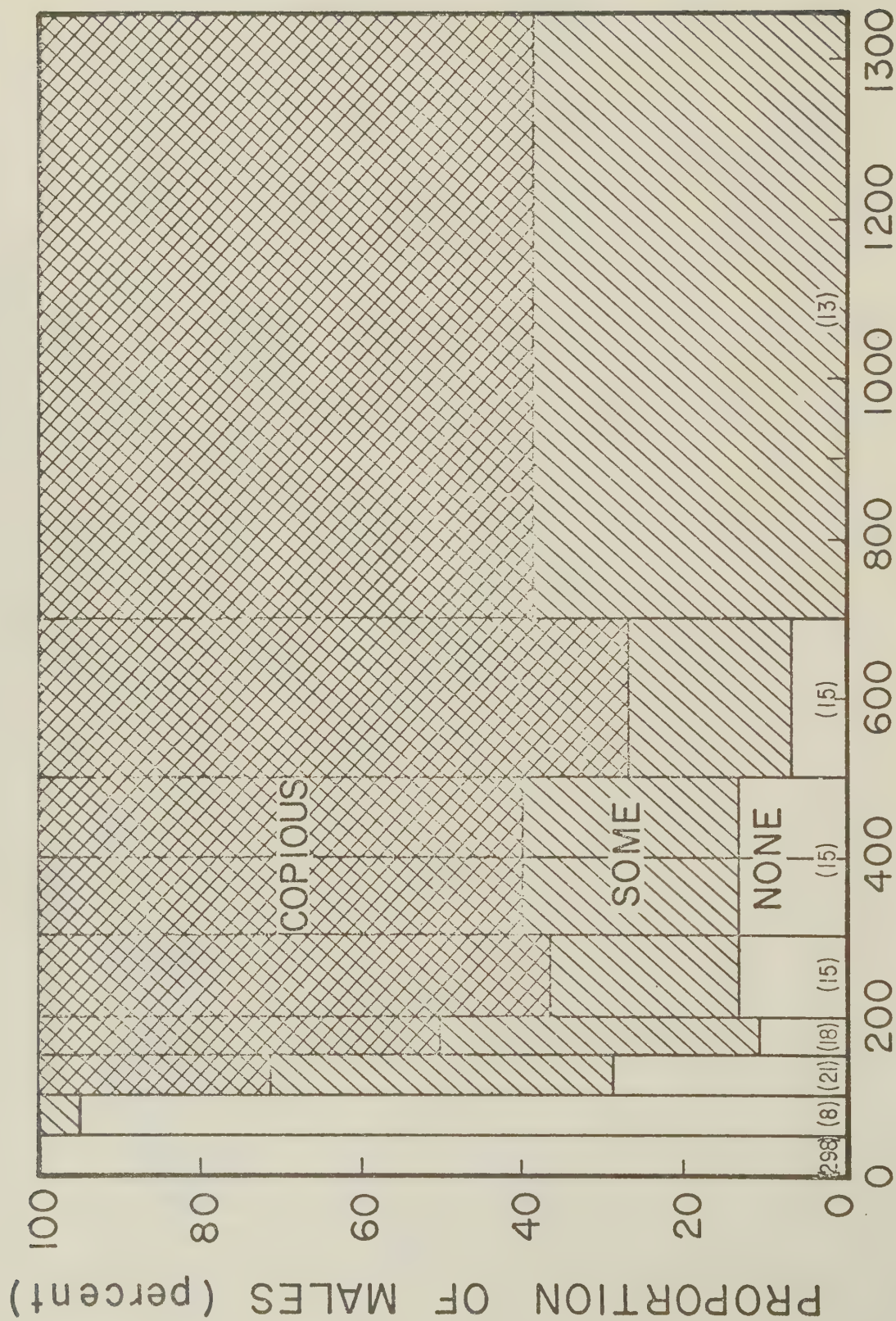


Figure 8. Linear regression analysis of relationship between testis-epididymis weight and proportion of males spermatogenic in the northern whitebelly spinner dolphin.



WEIGHT OF TESTIS & EPIDIDYMIS (g)

Figure 9. Amount of sperm in epididymis in relation to combined testis-epididymis weight in northern whitebelly spinner dolphin. Terms defined in Perrin et al. 1976. Sample sizes in parentheses. To be compared with Figure 18 in Perrin et al. 1977.

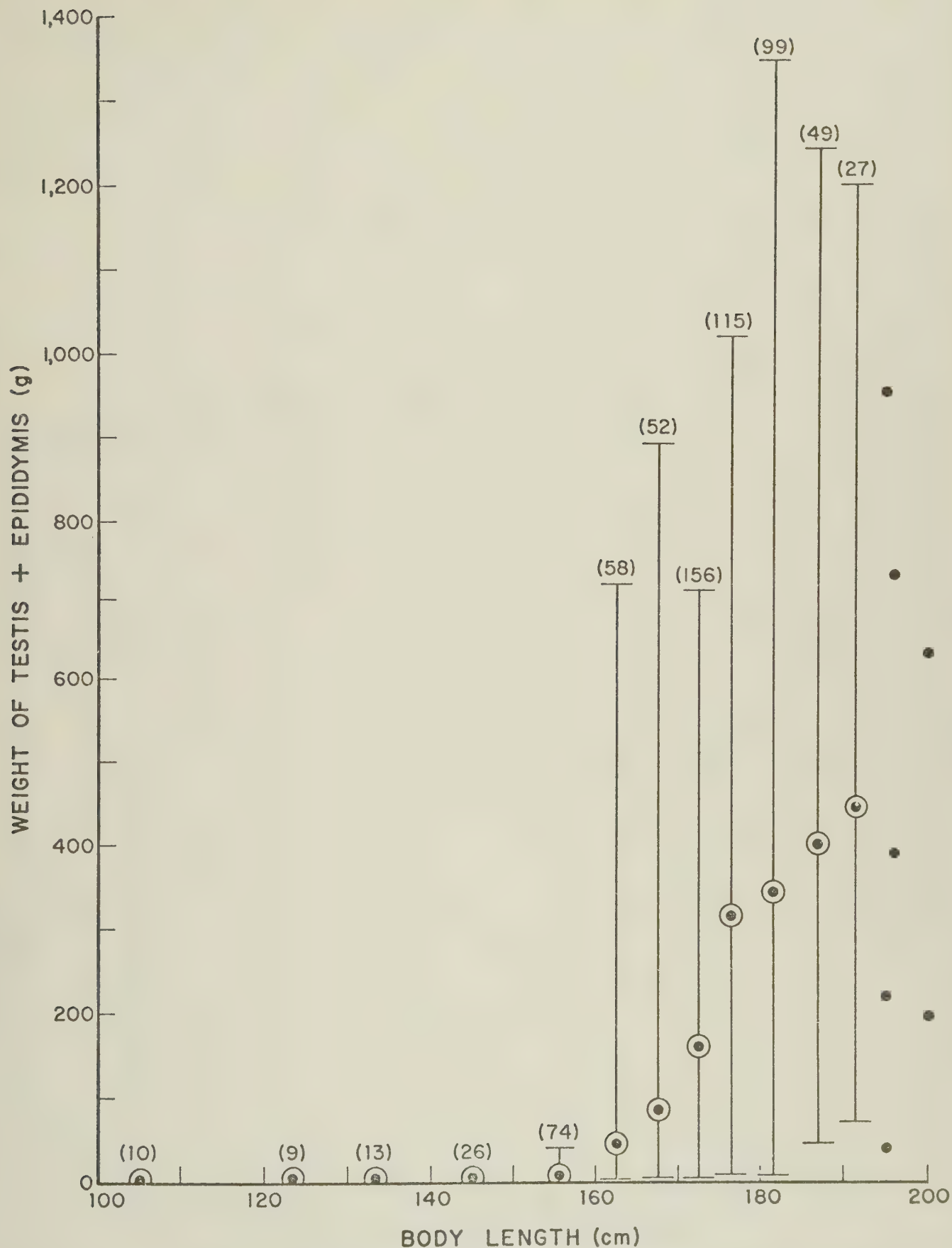


Figure 10. Relationship between testis-epididymis weight and body length in the northern whitebelly spinner dolphin. Sample sizes in parentheses. Circled dots are sample means; vertical bars are ranges.

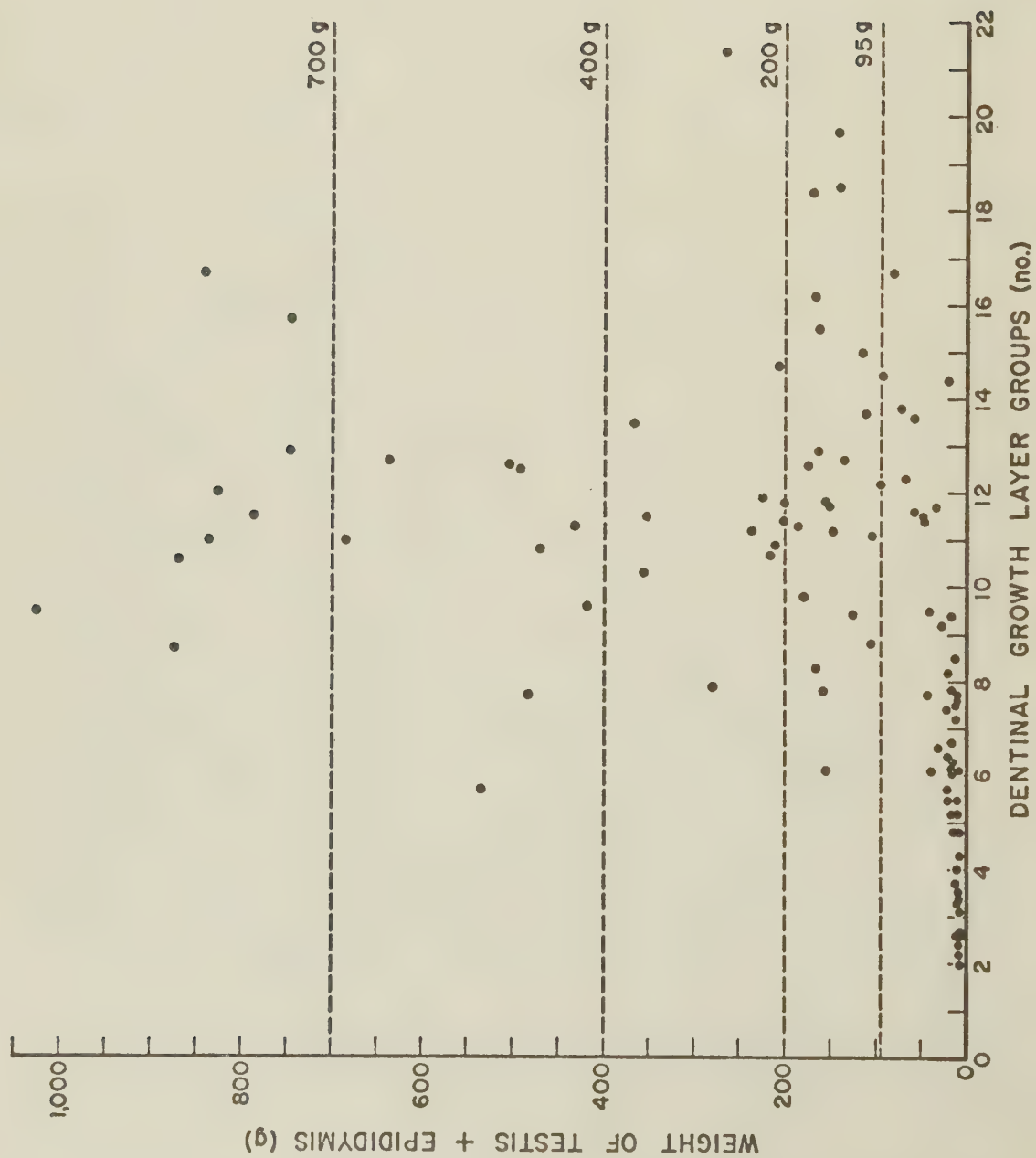


Figure 11. Scatter plot of testis-epididymis weight on age (in GLG s) for 102 northern whitebelly spinner dolphins.

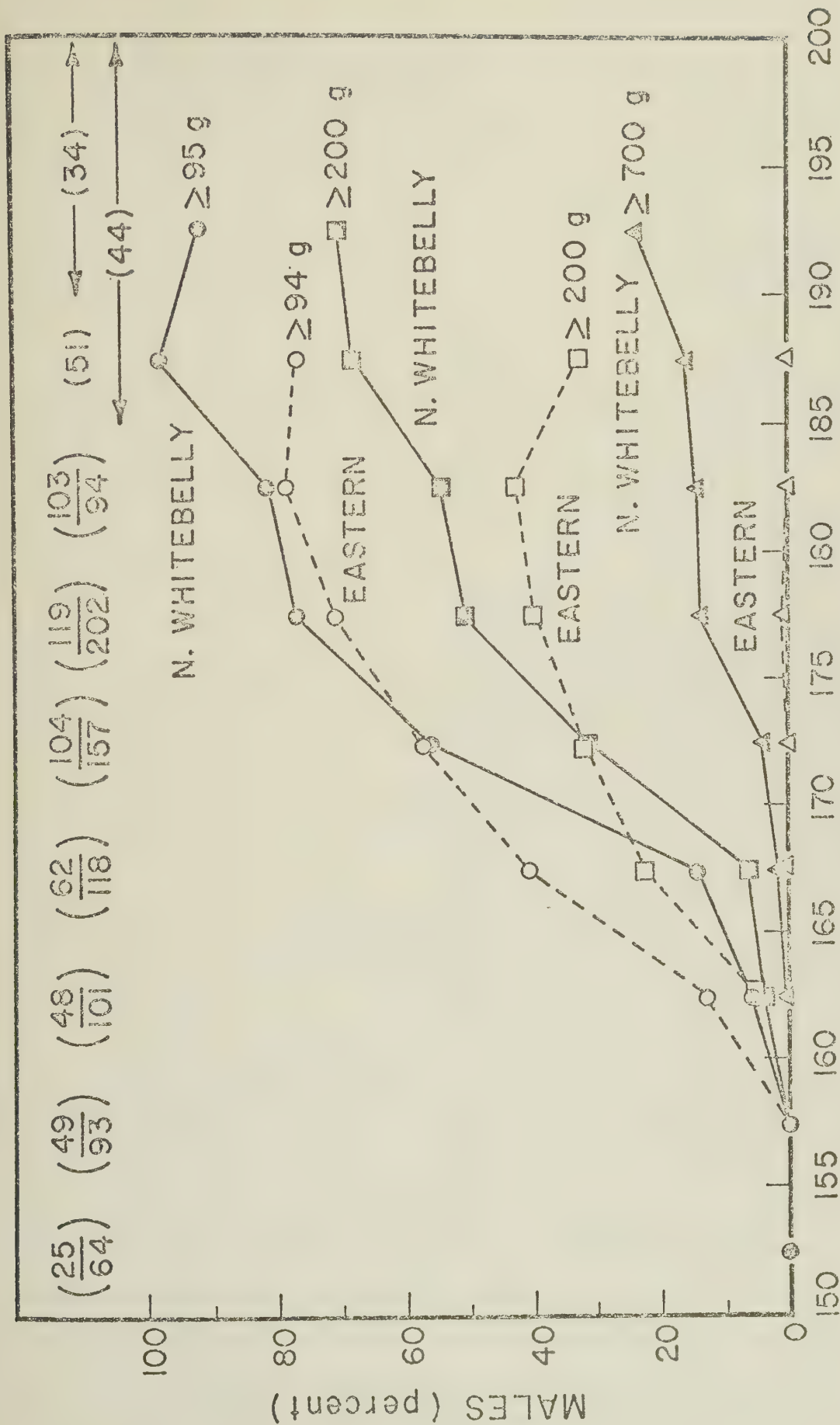


Figure 12. Proportion of males sexually "mature", in relation to body length under three criteria of testis-epididymis weight, in two populations of spinner dolphin: northern whitebelly spinner (solid lines) and eastern spinner (dashed lines). Sample sizes in parentheses (northern--bottom, whitebelly -- top).

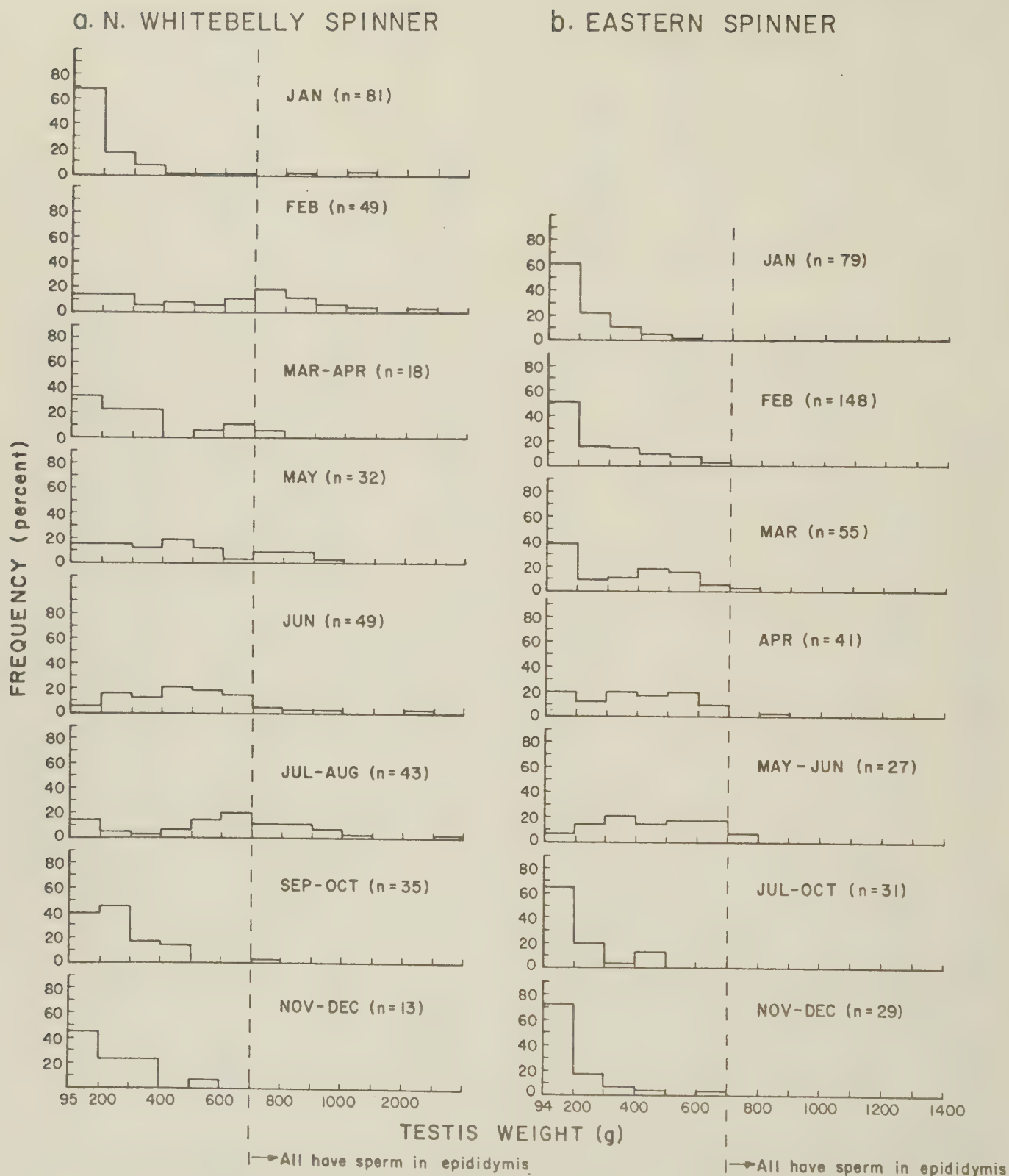


Figure 13. Testis-epididymis weight distribution by month in two populations of spinner dolphins. Data from 1968-1978; most from 1973-78.

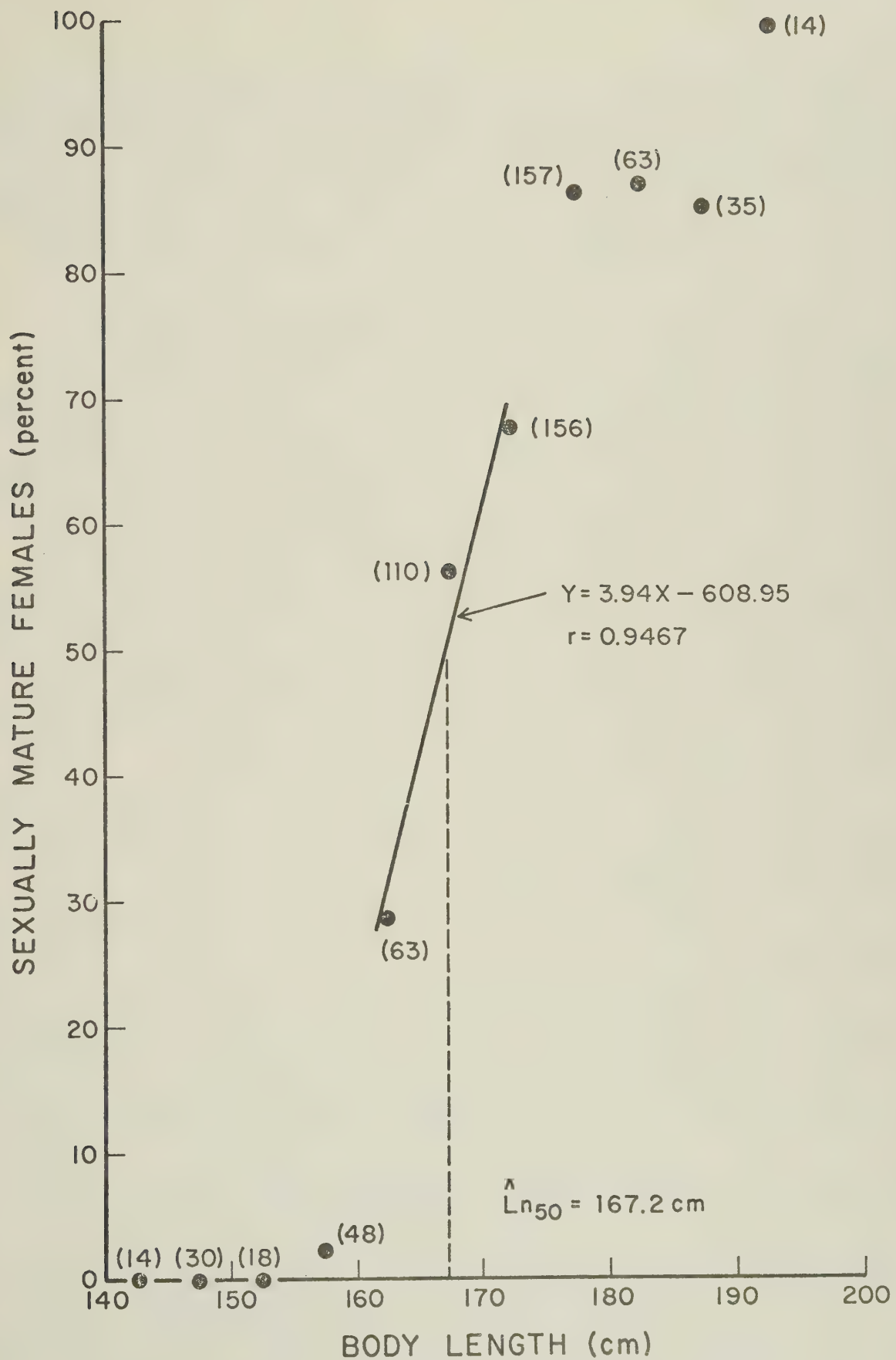


Figure 14. Estimation of body length at which 50% of female northern spinner dolphins show ovarian evidence of sexual maturity. Sample sizes in parentheses.

percent sexually mature are slightly asymmetrical (see Figure 22 in Perrin, et al. 1977), that is to say, there are more immature animals above the 50%-mature length than there are mature animals below it. This is caused by the confounding of developmental change in length with individual variation in length in the upper portion of the curves and results in an underestimate of average length of maturation. A correction is provided by using the length at which the mature-immature pattern is symmetrical. This point for the northern whitebelly spinner is 170cm and for the eastern spinner is 165cm, yielding estimates of age at maturation of 6.5 and 5.8 GLGs, respectively.

Another estimate of length at first conception can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Sixteen primiparous northern whitebelly females averaged 171.6 cm in length. Predicted age at that length is 6.94. The average length of their fetuses was 248 mm. This length is attained at about 4.3 months. Using the growth equations above to predict growth during 4.3 months for the various tooth-layering models and subtracting the growth increment of 171.6 cm yields estimates of length at first conception ranging from 169.7cm (6.4 GLGs) to 170.4cm (6.6 GLGs). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because some females may ovulate several times, and presumably continue to grow, before becoming pregnant the first time. Also, this method assumes no effect of pregnancy on growth rate. Average length of 16 primiparous eastern spinners (171.4cm) slightly exceeded the estimate of asymptotic size (170.9cm) used in the growth curve fit; an estimate from the growth equation, therefore, was not possible for the eastern spinner (probably indicating that the method is of dubious value).

Estimates of age at sexual maturity can also be derived directly from the smaller samples for which age determinations (GLGs in dentine) were made (Figure 15). The estimates are 5.3 GLGs in the eastern spinner and 6.7 GLGs in the northern whitebelly spinner.

The curves, although fit by eye to means for few and small samples, are quite different in form.

The largely independent different estimates of age (in GLGs) at maturation are not widely disparate (Table 3). Averaging of the estimates for the northern whitebelly spinner by Methods 2, 3, and 4 (Option II-1 GLG per year after first year), namely, 6.5, 6.7, and 6.6 GLGs, yields 6.6 GLGs, which value is used below. Averaging of the two relatively most reliable estimates available for the eastern spinner yields an estimate of 5.6 GLGs.

If it be assumed that one GLG is deposited after the first year (Hypothesis II in Table 3), female northern whitebelly spinners on the average mature at about 6 years of age and eastern spinners at about 5 years.

Ovulation Rate. Number of corpora in the ovaries (an index of reproductive history of the individual female dolphin) climbs sharply at about 6-7 GLGs in the northern whitebelly spinner (Figure 16) and at about 5-6 GLGs and more rapidly in the eastern spinner (Figure 6 in Perrin et al. 1977). To estimate ovulation rate, the required estimates of average reproductive ages for 2-GLG

Table 3. Results of analyses of length and age at attainment of sexual maturity in two populations of spinner dolphins. Values calculated with the growth equations are in parentheses.

Method (and comments)	Length (cm)		GLGs (no.)		Age (yr) under hypotheses		
	N.WB	EAST	N.WB	EAST.	I N.WB	II N.WB EAST.	III N.WB EAST.
1. Length at which 50% have corpora (probable underestimate)	167.2	164.1 ¹	(5.9)	(5.2)	3.9	5.5 4.7	4.2 ¹ 3.8 ⁵
2. Length at which mature below equals immature above (corrects for adult variation)	170.0	160.0 ²	(6.5)	(5.8)	4.3	6.0 5.3	4.8 4.4
3. Number of GLGs at which 50% have corpora (interpolation, but small sample sizes)	(170.8)	(164.2)	6.7	5.3 ¹	4.5	6.2 4.8	5.0 3.9
4. Length at first conception ³ , under hypothesis:	(169.7)	(---)	(6.4)	(---)	4.3	---	---
	(169.7)	(---)	(6.6)	(---)	---	6.1 (---)	---
	(170.4)	(---)	(6.6)	(---)	---	---	4.9 ⁴ (---)

1/ From Perrin et al. (1977)

2/ Includes data through 1978

3/ No estimates for the eastern spinner by this method; see text

4/ Switch from 1.5 to 1.0 GLG/yr assumed to occur at 161cm (5.41 GLGs)

5/ Ditto, at 157cm (4.13 GLGs)

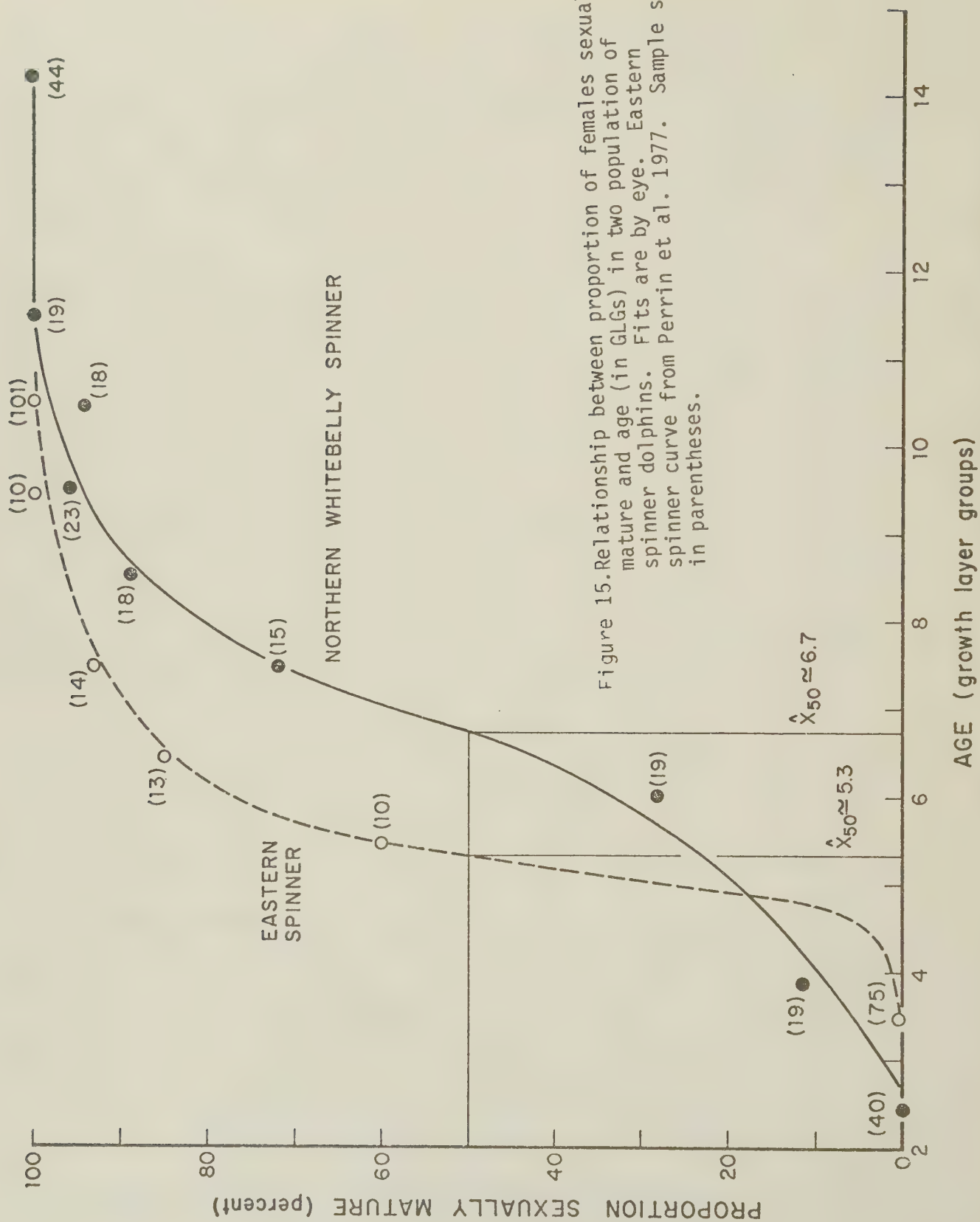


Figure 15. Relationship between proportion of females sexually mature and age (in GLGs) in two populations of spinner dolphins. Fits are by eye. Eastern spinner curve from Perrin et al. 1977. Sample sizes in parentheses.

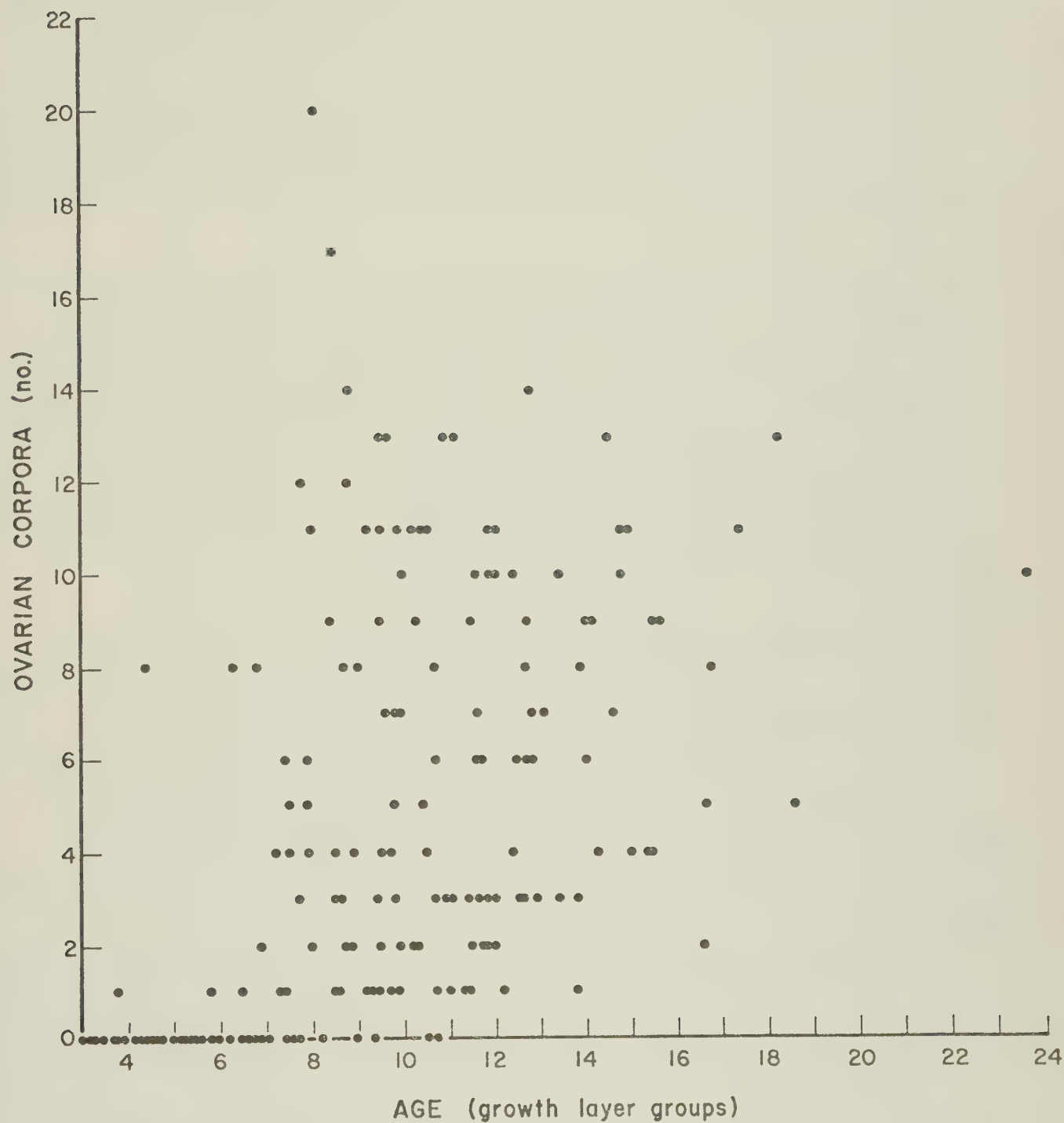


Figure 16. Scatterplot of number of ovarian corpora on age in GLGs in the northern whitebelly spinner dolphin.

intervals were calculated as in Perrin et al.(1977). Ovulation rates were estimated by fitting asymptotic curves to the 2-GLG interval means of average reproductive age (Figure 17) (assumes eventual cessation of ovulation in old females). Ovulation rate, as measured by these fits, in young females is higher in the northern whitebelly spinner than in the eastern spinner, but also levels off faster. The relative behavior of the two curves beyond about 8 GLGs of reproductive age may be greatly influenced by the small sample sizes involved at the higher ages, however, and all that can be said with some certainty is that during the first few years of reproductive life spinners in the eastern population ovulate less frequently than do those in the northern whitebelly population.

The shape of the corpora-count frequency distribution is an index of ovulation rate independent from the above fit to the corpora count on reproductive age. The distributions differ in the two populations (Figure 18), most markedly so between 0 and about 7 corpora. If it be assumed that mortality rates are about the same in the two populations over the span of reproductive age represented by about 7 corpora, the pattern of difference (higher frequency in the whitebelly population between one and four corpora and the reverse between four and seven corpora) can be explained by initial higher ovulation rate in the northern whitebelly population. The results of the two analyses agree quantitatively as well; the asymptotic fits (Figure 17) estimates that about seven corpora represents about the same reproductive span in the two populations, about seven GLGs (about seven years, if a one-GLG/year deposition rate is assumed).

Pregnancy Rate - Age-specific pregnancy rates, estimated as the proportion of reproductive females pregnant adjusted by length of gestation (10.6 mo), differ in the two populations (Figure 19). Between puberty and about age 10 GLGs, the pregnancy rate in the eastern population is 20-30% lower than in the northern whitebelly population. At about 11-13 GLGs, rate in the two populations are similar (about 35%), after which they decline, to about 20-25% in very old animals (post-reproductive females--senescent individuals with inactive ovaries--are not included in the samples). The samples are relatively small, but it seems clear that in young sexually adult females, which may make up a large proportion of the reproductive population, reproduction is less frequent in the eastern population than in the northern whitebelly population.

Gross production. - Gross annual reproductive rate, estimated as proportion of the population female X proportion of females sexually mature (and not post-productive) X annual pregnancy rate, did not differ between the two populations for the period 1973-78 (Table 4). Overall sex ratio was virtually identical in the two (very large) samples, about 0.96:1. The age structure of females, however, was quite different. Fifty-two percent of the northern whitebelly females were sexually mature, whereas only 43% of the eastern females were mature. The difference is statistically significant at $\alpha=0.05$. (A larger proportion of females were immature in the eastern than in the northern whitebelly samples for each year, 1973-1978 (Table 5)). Annual pregnancy rate was estimated by two methods, one in which the estimate of length of lactation is based on reproductive-condition structure of the sample of mature females and one in which the estimate of lactation is based on the length of the longest calf in a cumulative subsample of calves equal to the number of lactating females (Perrin et al. 1977). The latter estimate may be

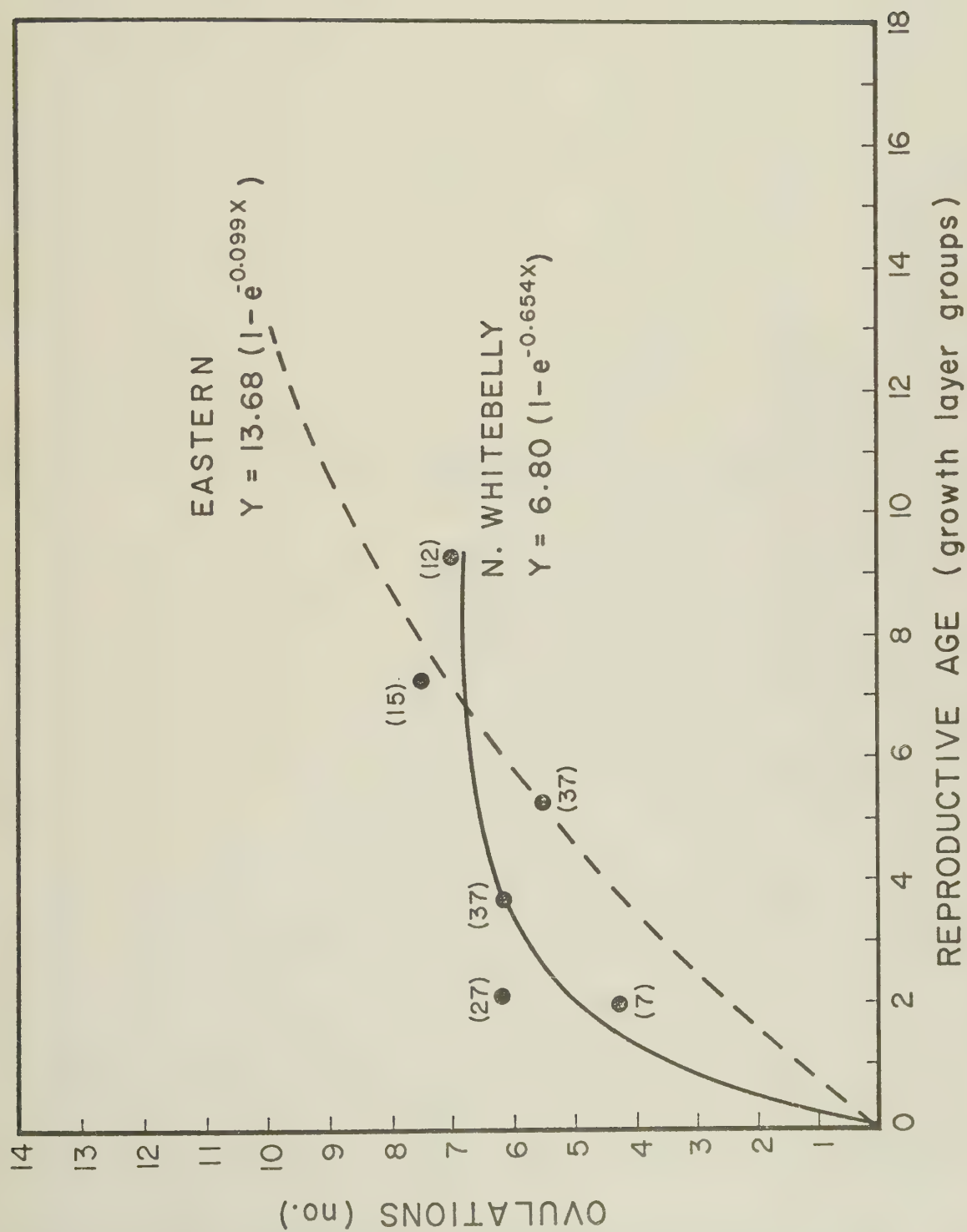


Figure 17. Asymptotic fit of corpora count on average reproductive age in the northern whitebelly spinner dolphin. Dashed line is asymptotic fit to data for eastern spinner (Figure 27 in Perrin, et al. 1977) Origin set at 0.001/0.001.

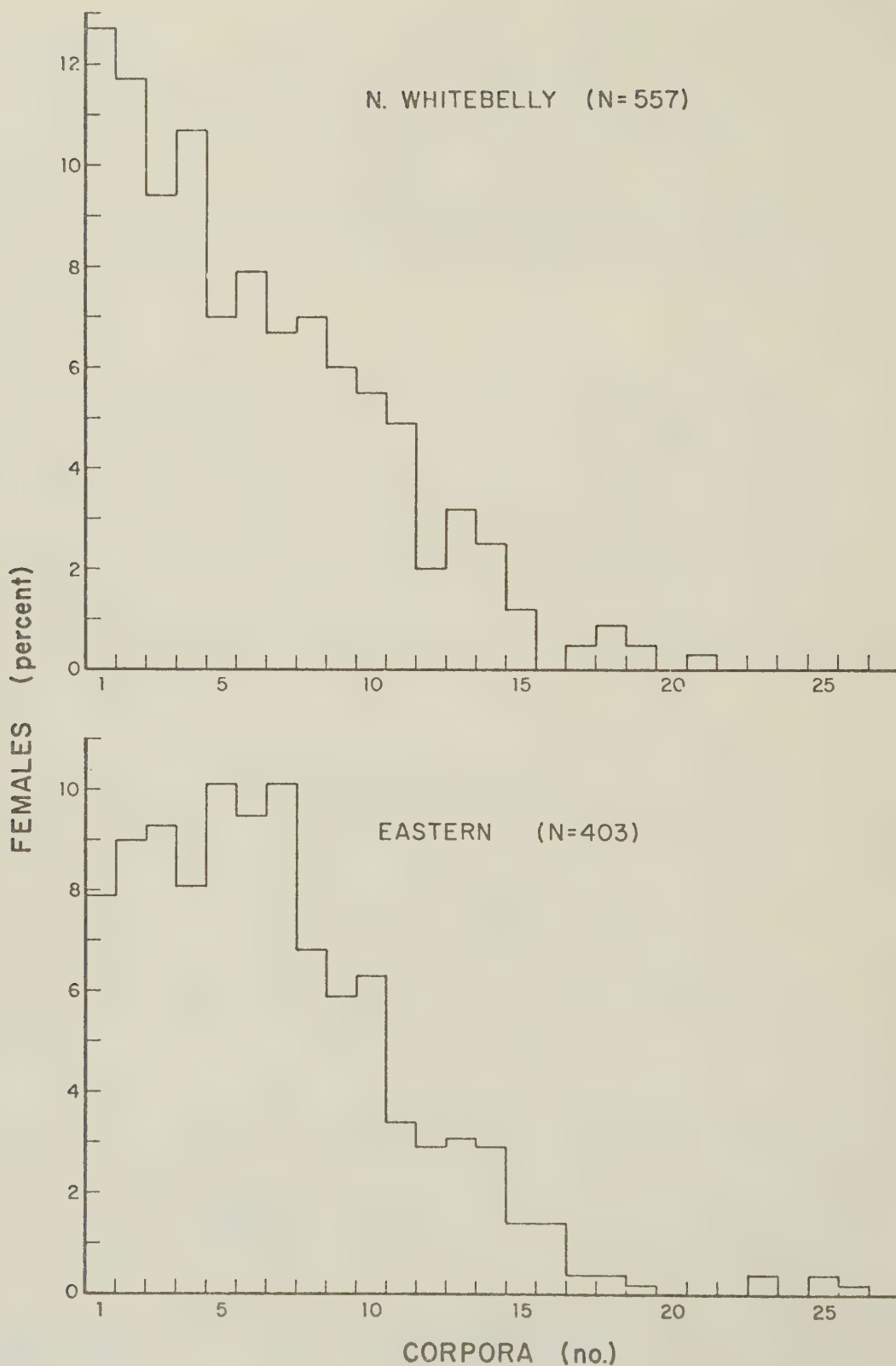


Figure 18. Frequency distribution of corpora count in two populations of spinner dolphins. Includes samples from 1973-78.

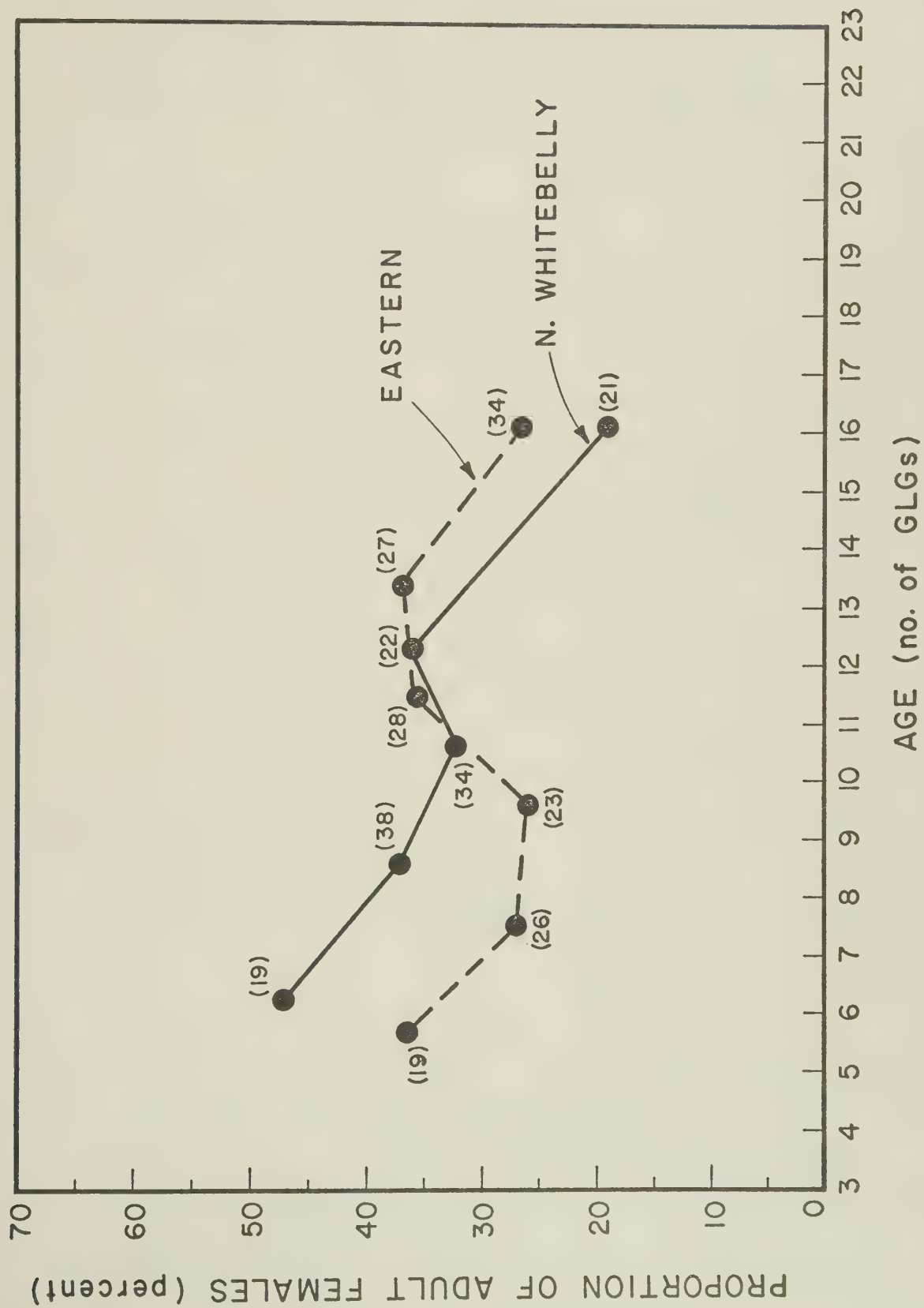


Figure 19. Age-specific pregnancy rates in two populations of spinner dolphins. Sample sizes in parentheses.

Table 4. Calculation of estimates of gross annual reproductive rates in two populations of spinner dolphins, based on pooled data for 1973-78.

Approximate 95% confidence limits are 2 S.E. (see loc. cit.). Sample sizes in parentheses. From Henderson et al. 1979.

	Northern white-belly spinner	Eastern spinner
A. Percent female	50.9 +2.4(1,778)	51.0 +1.8(2,938)
B. Percent females reproductive	52.2 +3.6(905)	43.2 +2.8(1,492)
C. Annual pregnancy rate (percent):		
by Method 1	35.6 +5.0(366)	33.9 +4.2(521)
by Method 2	33.2 +5.0(366)	44.6 +4.4(521)
A.xB.xC. Gross annual reproductive rate (percent):		
by Method 1	9.4 +1.4(1,631)	7.5 +1.0(2,624)
by Method 2	8.8 +1.4(1,631)	9.8 +1.2(2,624)

Table 5. Percentage of females sexually immature in two populations of spinner dolphins, 1973-78. Sample sizes in parentheses. From Henderson et al. 1979.

Year	Northern white-belly spinner	Eastern spinner
1973	48.9 (133)	54.4 (344)
1974	40.8 (49)	55.3 (396)
1975	45.5 (191)	57.0 (402)
1976	52.9 (191)	59.4 (106)
1977	48.2 (222)	59.7 (92)
1978	50.0 (118)	70.7 (92)

less biased than the former (loc. cit.).¹

The Method-1 estimate of pregnancy rate is about the same in the two populations, perhaps reflecting the above-discussed countervailing phenomena of (1) earlier age at maturity and (2) lower pregnancy rate in young adult females in the eastern populations. The Method-2 estimates, however, differ (significant at $\alpha=0.05$); overall pregnancy rate is higher in the eastern population. The method-2 estimate of gross production is slightly higher in the eastern than in the northern whitebelly population. The reverse is true for the Method-1 estimate. Neither of the differences, however, is statistically different.

DISCUSSION

Although differences exist between the northern whitebelly spinner and eastern spinner populations in several growth and reproductive parameters, there is no clear basis in the data available for assuming that historically greater exploitation of the eastern spinner population has resulted in higher gross reproductive rate. As would be expected, age at attainment of sexual maturity is lower in the eastern spinner population, possibly contributing to the shift in age structure toward younger animals. The pregnancy rate among young mature females, however, is also lower, possibly because of the lower proportion of fully mature males. The dearth of mature males hardly seems an adaptive population response and conceivably is a mechanical effect on male maturity structure (and perhaps age structure) by the purse-seining operation, through age- or maturity-selective fishing mortality, disruption of maturity-inducing social structure, or some other mechanism. In short, density-dependent populational response induced by the fishery may be counteracted by a more direct effect of the same fishery.

The various parameter estimates used here may be subject to sampling bias of various sorts. The bias in favor of calves in small-kill samples found in the case of the offshore spotted dolphin (Powers & Barlow, 1979) were not found to be significant in the spinner-dolphin samples, although that does not eliminate the possibility of systematic bias in sampling from kills of all

Footnote

¹/There is, however, a source of random error in the estimate that is not reflected in the binomial-based confidence interval. The age (from length) of the presumed longest-nursing calf in the sample is used as an estimate of length of lactation. This ignores individual variation in growth rate and doubtless individual variation in weaning age. In large samples, the random error would tend to convert to bias, as the inferred ages of the fastest-growing and longest-nursing calves consistently serve as the basis of the estimate, over-estimating length of lactation and underestimating annual pregnancy rate. The magnitude of the possible bias would be determined by the nature of variation in length at weaning. If weaning age is determined by body weight (length) rather than chronological age, the biases would tend to cancel out.

sizes. In any case, it can reasonably be assumed that whatever sampling biases exist are operating similarly for samples from the two populations. A possible exception to this is seasonal bias, as both reproduction and sampling are differentially seasonal (Barlow, 1979), but the effect, if any, can be presumed to be very small because of the length of gestation (almost a year) and the relatively diffuse nature of the reproductive seasonality.

The results here point out the need for further research on the biology of the two populations, particularly on age structure and on male reproductive functional morphology and physiology.

LITERATURE CITED

1. AU, D.K.W., W. PERRYMAN & W. F. PERRIN. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fisheries Center Admin. Rep. LJ-79-
2. BARLOW, J. 1979. Reproductive seasonality in pelagic dolphins of the eastern tropical Pacific. Doc. SOPS/79/26, Status of Porpoise Stocks Workshop, La Jolla, Calif., 27-31 Aug. 1979.
3. FOWLER, C. W. 1979. Non-linearity in population dynamics with special reference to large mammals. Document SOPS/79/14, Status of Porpoise Stocks Workshop, La Jolla, Calif., 27-31 August 1979.
4. FOX, W.W. 1978. The tuna-dolphin problem: five years of progress and future outlook. Oceans 11(3):57-59. Also in NMFS Tuna Newsletter, No. 58, May-June 1978. 6 p.
5. HENDERSON, J.R., W.F. PERRIN & R.B. MILLER. 1979. Gross annual production in dolphin populations (*Stenella* spp.) in the eastern tropical Pacific, 1973-78. Doc. SOPS/79/33, Status of Porpoise Stocks Workshop, La Jolla, Calif., 27-31 August 1979.
6. HASSELBLAD, V. 1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.
7. NOAA. 1977. Taking of marine mammals incidental to commercial fishing operations; final decision and final regulations. Federal Register 42(247):64547-64560.
8. PERRIN, W.F. 1969. Using porpoise to catch tuna. World Fishing 18(6):42-45.
9. PERRIN, W.F. 1975a. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. J. Fish.Res.Board Can.32:1059-1067.
10. PERRIN, W.F. 1975b. Variation of spotted and spinner porpoise (genus) *Stenella* in the eastern Pacific and Hawaii. Bull. Scripps Inst. Oceanogr. Univ. Calif. 21,206 p.
11. PERRIN, W.F., J.M. COE, AND J.R. ZWEIFEL. 1977. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull.,

U.S. 74(2):229-269.

12. PERRIN, W.F., D.B. HOLTS, AND R.B. MILLER. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75(4):725-750.
13. PERRIN, W.F. & A.C. MYRICK (eds.). 1980. Report of the workshop on age determination of odontocete cetaceans and sirenians, Sept. 1978. Rept. Int. Whal. Comm (in press)
14. PERRIN, W.F., P.A. SLOAN, and J.R. HENDERSON. 1979. Taxonomic status of the "southwestern stocks" of spinner dolphin, *Stenella longirostris* and spotted dolphin, *S. attenuata*. Rep. Int. Whal. Comm 29:175-184.
15. POWERS, J.E. and J. BARLOW. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, Status of Porpoise Stocks Workshop, 27-31 August 1979, La Jolla, Calif.
16. Southwest Fisheries Center. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. (La Jolla, July 27-31, 1976). SWFC Admin. Rep. No. LF-76-29.
17. ZWEIFEL, J. and W.F. PERRIN. 1980. Fitting curves to odontocete length/tooth layer data. Proc. Int. Conf. Age Determin. Odont. Cetaceans and Sirenians. Rep. Int. Whal. Comm. (in press).

